

Assessing wood properties in standing timber with laser scanning

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ACADEMIC DISSERTATION

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Title of dissertation: Assessing wood properties in standing timber with laser scanning

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Dissertationes Forestales 295

<https://dx.doi.org/df.295>

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ISSN 1795-7389 (online)

ISBN 978-951-651-680-9 (pdf)

ISSN 2323-9220 (print)

ISBN 978-951-651-681-6 (paperback)

Cover: Jiri Pyörälä

Printers: Unigrafia, Helsinki 2020

Publishers:

Finnish Society of Forest Science

Faculty of Agriculture and Forestry at the University of Helsinki

School of Forest Sciences of the University of Eastern Finland

Editorial Office:

Finnish Society of Forest Science, Viikinkaari 6, FI-00790 Helsinki, Finland

<http://www.dissertationesforestales.fi>

Pyörälä, J. (2020). Assessing wood properties in standing timber with laser scanning. *Dissertationes Forestales* 295. 52 p. <https://doi.org/10.14214/df.295>

ABSTRACT

Managed forests play crucial roles in ongoing climatic and environmental changes. Among other things, wood is capable of sinking and storing carbon in both standing timber and wood products. To promote these positive effects, more precise planning is required that will ensure sustainable forest management and maximal deposition of harvested wood for long-term applications. Information on wood properties plays a key role; i.e. the wood properties can impact the carbon stocks in forests and the suitability of wood for structural timber.

With respect to the theoretical background of wood formation, stem, crown, and branching constitute potential inputs (i.e. wood quality indicators) to allometric wood property, tree biomass, and wood quality models. Due to the complex nature of wood formation, measurements of wood quality indicators that could predict wood properties along the relevant directions of variation have previously been elusive in forest inventories. However, developments in laser scanning from aerial and terrestrial platforms support more complex mapping and modeling regimes based on dense three-dimensional point clouds.

The aim here was to determine how wood properties could be estimated in remote-sensing-aided forest inventories. For this purpose, methods for characterizing select wood quality indicators in standing timber, using airborne and terrestrial laser scanning (ALS and TLS, respectively) were developed and evaluated in managed boreal Scots pine (*Pinus sylvestris* L.) forests. Firstly, the accuracies of wood quality indicators resolved from TLS point clouds were assessed. Secondly, the results were compared with x-ray tomographic references from sawmills. Thirdly, the accuracies of tree-specific crown features delineated from the ALS data in predictive modeling of the wood quality indicators were evaluated.

The results showed that the quality and density of point clouds significantly impacted the accuracies of the extracted wood quality indicators. In the assessment of wood properties, TLS should be considered as a tool for retrieving as dense stem and branching data as possible from carefully selected sample trees. Accurately retrieved morphological data could be applied to allometric wood property models. The models should use tree traits predictable with aerial remote sensing (e.g. tree height, crown dimensions) to enable extrapolations.

As an outlook, terrestrial and aerial remote sensing can play an important role in filling in the knowledge gaps regarding the behavior of wood properties over different spatial and temporal extents. Further interdisciplinary cooperation will be needed to fully facilitate the use of remote sensing and spatially transferable wood property models that could become useful in tackling the challenges associated with changing climate, silviculture, and demand for wood.

Keywords: Wood quality, Precision forestry, Forest management, Remote sensing

PREFACE

Back in early 2014, I was finishing my Master's Degree in wood technology. My Master's thesis on wood properties in uneven-aged spruce had been my first peek into studying the complexity of wood formation. I found it mysterious how trees communicate with the environment through series of processes that from an animal perspective are curiously slow and permanent, and how they produce wood that is equally intriguing as a material. I was searching for a research project that would keep me close to these topics, and eventually, got lured into a PhD position with initial title "Measuring wood quality with terrestrial laser scanning" by my supervisors Markus Holopainen and Marketta Sipi. With precious help from them and Mikko Vastaranta, we applied for research funding.

Meanwhile, I was hired by Finnish Geodetic Institute (later Finnish Geospatial Institute, FGI) for field work in summer 2014 in Evo, Hämeenlinna. Harri Kaartinen introduced me to laser scanning and geographic measurements that laid the groundwork for later data acquisitions. I continued working in FGI with Xinlian Liang, who introduced me to the point cloud processing and quantitative point cloud analyses that became extremely useful later.

After receiving personal funding, I started working on the first research paper in autumn 2015, and it was submitted by spring 2016. That paper never got accepted, and I had to completely rewrite it. The first paper was finally accepted in late 2017. In hindsight, I'm glad things went that way, as it was an educating lesson in academic writing. I am grateful to Mikko and Ville Kankare who helped me struggle through that first endeavour. In the subsequent studies, I worked my way through various aspects of data processing, algorithm development and study design considerations with irreplaceable aid from my senior co-authors, Xinlian, Yunsheng Wang, Ninni Saarinen, Ville and Mikko.

With this thesis, I believe I've come full circle back at the questions of wood formation that got me into research in the first place. I am now looking forward to using the new skills acquired in this project, to ask the questions that still keep me agitated—how trees make wood, and how it all links to our place in the cycle, as active inhabitants and tenders of forests and users of wood.

It goes without saying that there exists a great number of people, both peers and colleagues as well as friends and family that deserve acknowledgement.

First, I wish to express my greatest gratitude to my supervisor and group leader Markus, for his genuine support and trust towards my work. In continuation to that I thank our research group that makes the everyday work so enjoyable (including lunch times, social events and work trips): Mikko, Ville, Ninni, Ville L., Samuli, Topi, Einari, Mohammad and Tuomas. I am also grateful to everyone at FGI who have been involved: Juha Hyypä, Xinlian, Yunsheng, Harri, Antero and Matti L., as well as to those from the Department of Forest Sciences: my supervisor Marketta and Juha R. who is always just one door down the hall when I need to ask something about wood, and Veli-Pekka for his kind support. I also want to thank warmly Riikka Piispanen, Sauli Valkonen and Pekka Saranpää from Natural Resources Institute Finland (Luke)—although not participants in the PhD project, they sparked my interest towards wood formation in the first place, during the Master's thesis project. Then I must give special mention to Nicholas Coops and everyone in his lab in University of British Columbia, where I had the privilege to spend four months in 2018. Observing the way Nicholas worked with his lab opened me whole new perspectives in scientific thinking—not to forget the Friday beers and other social events outside of work.

The following agencies are gratefully acknowledged for financial support: Jenny ja Antti Wihurin rahasto, Suomen Luonnonvarain Tutkimussäätiö, Suomen Metsäsäätiö, Ministry of Agriculture and Forestry, and Academy of Finland. Dr. James Thompson is acknowledged for editing the language of the thesis.

Another important aspect in my life has always been music. Based on my experience, art and science are highly similar, creative processes that mutually boost my involvement with one and another. Great cheers to all my band mates Markus, Jaakko, Aaro, Rolle, Teemu and Osmo!

Finally, there are a bunch of people with whom I share various aspects of my life to varying extents, and to whom I want to give my greatest thanks for simply being there throughout the years: Pauliina the Conqueror of my Space and Time, my mother and grand parents who taught me the appreciation for nature, Jori, Suvi, Johanna, Janina and all other relatives, Pauli, Tommi, Joonas, Pentti, Paul, Janne, Tuomo, Hannele, Lauri and Pihla E., to name just few.

Helsinki, April 2020
Jiri Pyörälä

LIST OF ORIGINAL PUBLICATIONS

This study is based on the following articles referred to in the text by their Roman numerals, as well as on unpublished results. The papers are reproduced with permission provided by the publishers.

I Pyörälä, J.; Kankare, V.; Vastaranta, M.; Rikala, J.; Holopainen, M.; Sipi, M.; Hyypä, J.; Uusitalo, J. (2018a). Comparison of terrestrial laser scanning and x-ray scanning in measuring Scots pine (*Pinus sylvestris* L.) branch structure. *Scandinavian Journal of Forest Research* 33(3), 291-298. <https://doi.org/10.1080/02827581.2017.1355409>

II Pyörälä, J.; Liang, X.; Vastaranta, M.; Saarinen, N.; Kankare, V.; Wang, Y.; Holopainen, M.; Hyypä, J. (2018b). Quantitative assessment of Scots pine (*Pinus sylvestris* L.) whorl structure in a forest environment using terrestrial laser scanning. *IEEE Journal of Selected Topics in Applied Earth Observations and Remote Sensing* 11(10), 3598-3607. <https://doi.org/10.1109/JSTARS.2018.2819598>

III Pyörälä, J.; Liang, X.; Saarinen, N.; Kankare, V.; Wang, Y.; Hyypä, J.; Holopainen, M.; Vastaranta, M. (2018c). Assessing branching structure for biomass and wood quality estimation using terrestrial laser scanning point clouds. *Canadian Journal of Remote Sensing* 44(5), 462-475. <https://doi.org/10.1080/07038992.2018.1557040>

IV Pyörälä, J.; Kankare, V.; Liang, X.; Saarinen, N.; Rikala, J.; Kivinen, V-P.; Sipi, M.; Hyypä, J.; Holopainen, M.; Vastaranta, M. (2019a). Assessing log geometry and wood quality in standing timber using terrestrial laser-scanning point clouds. *Forestry* 92(2), 177-187. <https://doi.org/10.1093/forestry/cpy044>

V Pyörälä, J.; Saarinen, N.; Kankare, V.; Coops, N.; Liang, X.; Wang, Y.; Hyypä, J.; Vastaranta, M. (2019b). The variability of wood properties using terrestrial and airborne laser scanning. *Remote Sensing of Environment* 235, 111474. <https://doi.org/10.1016/j.rse.2019.111474>

AUTHOR CONTRIBUTION

Jiri Pyörälä wrote the first versions of all manuscripts and was responsible for carrying out the majority of data acquisition, measurements, data processing, and statistical analyses in all research articles (I-V). Jiri Pyörälä developed the quantitative branch detection and modeling algorithm jointly with Xinlian Liang (II). The studies were designed jointly among all coauthors, and all coauthors participated in revising the final manuscripts (I-V).

CONTENTS

ABBREVIATIONS	8
1. INTRODUCTION.....	9
1.1. Background	9
1.2. Wood properties in forest management and use	9
<i>1.2.1. Wood formation and wood properties.....</i>	<i>9</i>
<i>1.2.2. Effect of forest management on tree morphology and wood properties</i>	<i>12</i>
<i>1.2.3. Forest biomass</i>	<i>12</i>
<i>1.2.4. Wood quality.....</i>	<i>13</i>
1.3. Laser scanning of wood properties in forest management and use	14
<i>1.3.1. Remote sensing of forests and the role of laser scanning...14</i>	<i>14</i>
<i>1.3.2. Airborne laser scanning—mapping canopy structures and growth conditions.....15</i>	<i>15</i>
<i>1.3.3. Terrestrial laser scanning—detailed geometrical models of tree morphologies</i>	<i>17</i>
1.4. Thesis scope and objectives	19
2. MATERIALS AND METHODS.....	19
2.1. Study areas, sample trees, and plots.....	19
2.2. Reference data.....	20
<i>2.2.1. Field measurements</i>	<i>20</i>
<i>2.2.2. Sawmill measurements.....</i>	<i>20</i>
2.3. Study data	21
<i>2.3.1. Terrestrial laser-scanning data acquisition and preprocessing</i>	<i>21</i>
<i>2.3.2. Terrestrial laser-scanning point cloud-based geometrical tree-modeling methods</i>	<i>22</i>
<i>2.3.3. Airborne laser-scanning data acquisition, feature extraction, selection, and modeling</i>	<i>22</i>
2.4. Statistical analyses	23
3. RESULTS AND DISCUSSION	25
3.1. Summary of the results in the original articles	25
3.2. Methodological considerations and restrictions	28
3.3. Applications in the modeling of wood properties and wood quality	30
3.4. Implications for forest management and use.....	32
4. CONCLUSIONS.....	33
REFERENCES	34

ABBREVIATIONS

2-D, 3-D	Two-dimensional, three-dimensional
ALS	Airborne laser scanning
CHM	Canopy height model
<i>DBH</i>	Diameter-at-breast height (1.3 m above ground)
DSM	Digital surface model
DTM	Digital terrain model
EW	Earlywood
<i>G</i>	Basal area
<i>H</i>	Tree height
<i>H_{db}</i>	Lowest dead branch height
<i>H_{dom}</i>	Dominant height (mean <i>H</i> of 100 largest trees in <i>DBH</i> on hectare)
<i>H_{lc}</i>	Live crown base height
ITD	Individual tree delineation
LW	Latewood
<i>MBD</i>	Maximum branch diameter
ME, MD	Mean error, mean difference, or bias
<i>MFA</i>	Microfibril angle
MLS	Mobile laser scanning
PCA	Principal component analysis
RANSAC	Random sample consensus
RF	Random forest
RMSE	Root-mean-squared error
TLS	Terrestrial laser scanning
UAV	Unmanned aerial vehicle
<i>V_{sawlog}</i>	Volume of sawlog section (diameter > 15 cm)

1. INTRODUCTION

1.1. Background

Forests play several roles in global environmental, climatic, and social changes (Bonan 2008; Cardinale et al. 2012; Foley et al. 2005; Law et al. 2018; Luyssaert et al. 2018). They are natural habitats for approximately 75% of land animals and plants and storages of 50% of the terrestrial carbon that can remove 15–30% of the annual anthropogenic CO₂ emissions from the atmosphere (Arneth et al. 2017; Pan et al. 2011). However, these global changes and unsustainable forest use together pose serious threats of forest degradation or deforestation in many regions that may yet undermine the potential attributed to forests (Sasaki and Putz 2009). Optimal utilization of forest resources, including the substitution of wood for steel, concrete, and plastics in long-term deposits is one crucial factor in net-positive carbon sequestration in managed forests, especially when the demand for wood is increasing (Jonsson et al. 2018). The capacity of forests and industrial forestry to live up to their potential is thus influenced by the decisions made in forest management and use (Canadell and Raupach 2008; Vauhkonen and Packalen 2018).

By estimation, approximately 50% of global forested areas are under a management plan, either for wood production (~30% of the forested area), conservation (~20%), or multiple purposes (~25%, overlapping with the previous numbers) (MacDicken et al. 2016). In Finland, approximately 90% of forests are managed for wood production (Peltola 2014). In countries such as Finland, where forestry and the forest industry are highly developed, the forest sector is expected to preserve the forest carbon storage and uptake as well as biodiversity, while also securing sustainable wood production in answer to the increasing demand. Various authors have stated that improvements in the value-added of wood and the precision and flexibility of management, planning, harvests, logistics, and end production are required for better accounting of the multiple goals set for forestry (Gardiner and Moore 2014; Holopainen et al. 2014; MacKenzie and Bruemmer 2009).

Detailed, accurate, and timely planning of forest management and wood procurement requires information on forest growth and structure with high spatial and temporal resolution. Fortunately, high-resolution remote-sensing data from various sensors and platforms are becoming more commonly available for forest inventorying (Liang et al. 2016; Liang et al. 2018b; Liang et al. 2019; Réjou-Méchain et al. 2019; Wästlund et al. 2018). Much of the potential remains untapped, and research is needed to facilitate the use of remote sensing in increasingly complex mapping and modeling applications. One of the application fields requiring development is the estimation of wood properties in standing timber. Wood properties such as wood density and fiber dimensions can highly affect forest biomass and wood quality, i.e. the carbon stored in wood both in standing timber and that manufactured into long-term deposits. Precise inventory data on wood properties would support more precise planning and decision making in forest management and use.

1.2. Wood properties in forest management and use

1.2.1. Wood formation and wood properties

By definition, wood is a “hard fibrous substance that makes up the greater part of the stems, branches, and roots of trees or shrubs (and some herbaceous plants) beneath the bark” (Anon 2019). Wood is responsible for the structural support, water transport, and nutrient storage of

plant bodies. In forestry, wood more specifically refers to the secondary xylem in the stems of gymnosperms and dicot angiosperms, i.e. coniferous and broad-leaved trees, or softwoods and hardwoods, respectively. In the context of this thesis, wood properties refer to the anatomy and functionality of stem wood: cell dimensions, wood density, microfibril angle (*MFA*), and knottness.

Wood properties are determined during wood formation, which includes primary and secondary growth in apical and lateral meristems (stem apex and cambium, respectively). Primary growth is responsible for the longitudinal growth of the stem apex and branch tips and the initiation of the cambium envelope around the primary xylem (or pith). Secondary growth is responsible for the transversal growth of stems and branches, since the cambium produces secondary xylem (or sapwood) inwards, and phloem and bark outwards. Tracheary cells—tracheids, vessels, and fibers—are responsible for water transport and structural support and comprise up to 90% of the sapwood in most forest trees.

Five stages of secondary growth are often distinguished in the tracheary cells (Rathgeber et al. 2016): (1) cell division, (2) cell expansion, (3) cell-wall thickening, (4) lignification, and (5) programmed cell death. Primary growth regulates secondary growth through molecular signaling, i.e. by transporting phytohormones and nonstructural carbohydrates (photosynthates) basipetally through the vascular cambium (Larson 1969; Sorce et al. 2013). The most important implications for wood properties in the context of this thesis is how the signaling determines the predomination of any of the first three stages: cell division, expansion, and cell-wall thickening (Björklund et al. 2017; De Rybel et al. 2016; Ugglä et al. 1996). These processes fundamentally affect the anatomy and functioning of wood, e.g. wood density, which is constituted by lumen diameters and the thickness of cell walls. The regulation of secondary growth is pivotal for the adaptability of wood to extrinsic changes in climate and the environment, as well as to intrinsic changes in hydraulic maintenance and structural support as the tree grows (Cabon et al. 2020; Petit et al. 2018; Pullen et al. 2019; Spicer and Groover 2010; Vaganov et al. 2006).

In boreal and temperate regions, the seasonally variable temperature, soil moisture, and day length control primary growth, photosynthesis, and hormonal activity in trees and affect the timing, duration, and rate of the secondary growth stages (Begum et al. 2013; Schrader et al. 2003). The implications are most apparent in the annual ring patterns of many boreal and temperate gymnosperms, with distinctive transitions from earlywood (EW) to latewood (LW). EW tracheids in gymnosperms are relatively short, with large lumen size and thin cell walls, and they function as conduits for the ascending sap. LW tracheids are longer, narrower, and have thicker cell walls, mainly serving in mechanical support functions. To give an example of the dependencies between secondary and primary growth, several studies have reported that the rates of primary and secondary growth both peak around the summer solstice in temperate and boreal gymnosperms, and coincide with EW to LW transitioning (Cuny et al. 2015; Huang et al. 2014; Ugglä et al. 2001), and the variation in both radial and vertical increments indicate similar environmental signals (Mäkinen 1998).

In addition to annual fluctuations, tree age, size, and structure highly affect secondary growth over time. Stem wood produced by a young cambium within a live crown is called juvenile wood (or crown wood, or core wood), and that produced by older cambium below the crown is called mature wood (or stem wood, or outer wood). Juvenile wood is often distinguished by its smaller wood density, lower lignin content, smaller tracheids, and steeper *MFA* than mature wood, although there is continual debate over the terms and their definitions (Amarasekara and Denne 2002; Burdon et al. 2004; Eberhardt et al. 2019). In short, the combination of apical and cambial ageing, increasing tree height (*H*) and crown

size, ascending base height of live crown (H_{lc}), and the increasing pressure on the cambium due to increasing tree size gradually transform the wood produced (Amarasekara and Denne 2002; Kucera 1994; Lundqvist et al. 2018; Mansfield et al. 2007). Consequently, vertical and radial developments of several wood properties in the xylem exhibit well-established relationships with H and stem radius (Auty et al. 2014b; Eberhardt et al. 2019; Lachenbruch et al. 2011) as reflections of wood formation adapting to changing canopy dynamics and tree morphology over time, hence giving rise to the terms ‘juvenile’ and ‘mature’ wood (Figure 1). The properties and proportions of EW, LW, juvenile, and mature wood comprise the baseline for intra-tree variabilities of wood properties that further vary between forest types, different forest management regimes, and climatic domains.

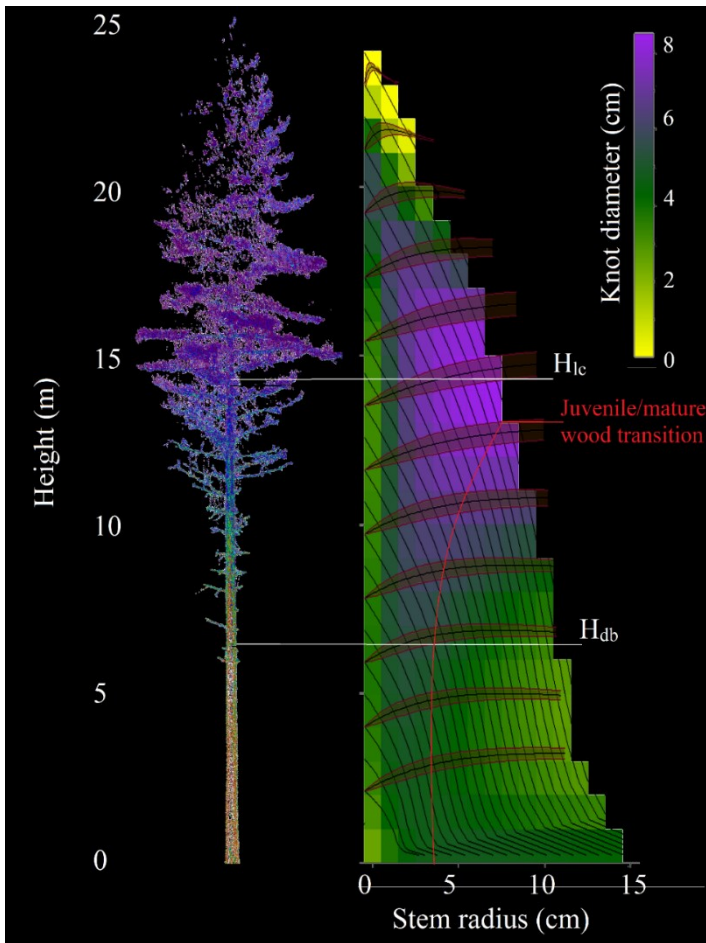


Figure 1. Schematic illustration of vertical and radial variabilities of mean knot diameters (as a wood property) and their relationships with stem geometry and branching. The allometric relationships between longitudinal and radial increments of the stem and branches reflect past growth with implications for the wood formed. The transitioning from juvenile to mature wood is related to the ascending base height of the live crown (H_{lc}). The mean knot diameter gradient thus reflects intra-tree variabilities of other wood properties, e.g. wood density and fiber dimensions. Tree-to-tree fluctuations in the baseline variation arise from differences in canopy positions, stand conditions, and climate. H_{db} = Height of the lowest dead branch.

1.2.2. *Effect of forest management on tree morphology and wood properties*

Trees have some of the longest lifespans of all living organisms, as well as very slow metabolism. The explicit effects of forest management practices on wood formation processes may therefore appear negligible, but become significant when they accumulate over decades or centuries. The interactions of species-specific shade tolerance, climatic adaptability, and crown plasticity with climate, environmental conditions, and forest management are pivotal to the development of tree morphology and wood properties (Babst et al. 2019; Pretzsch and Rais 2016). Forest management interferes with wood formation by favoring trees with select morphological traits and altering the environmental setting with implications for the biological interdependencies between primary and secondary growth. These effects are manifested in allometric relationships in tree morphology that are well-known and commonly used to guide decision making in forest management and planning (West et al. 1999).

In the context of this thesis, the allometry of crown and branching plays a particularly intriguing twofold role. On one hand, branches become knots that are important wood properties as such (Björklund 1997; Moberg 2006). On the other hand, the crown and branches in many ways also reflect other wood properties related to the EW:LW ratio and maturity of wood (Eberhardt et al. 2019; Huang et al. 2014; Kuprevicius et al. 2013; Pamerleau-Couture et al. 2019) (Figure 1). Increasing site fertility and decreasing stocking density (or canopy packing) have been linked with increased crown longevity and stem taper (Benjamin et al. 2009; Huuskonen et al. 2014; Mäkinen 1999; Pothier et al. 2013), which are signals of increased radial growth rates and EW and juvenile wood contents (Auty et al. 2018; Cortini et al. 2013; Lindström 1996; Moore et al. 2009; Pokharel et al. 2014).

For example, intensive forest management actions accompanied by short rotations have evidently increased juvenile growth rates in industrially cultivated forest stocks, resulting in decreases in wood density, timber stiffness, and strength (Moore and Cown 2017; Zhang 1995; Zobel 1984). On the other hand, relatively little is known about the variabilities of wood properties in uneven-aged and mixed-species forests where the canopy conditions are more diverse (Pamerleau-Couture et al. 2019; Piispanen et al. 2014; Pretzsch and Rais 2016; Zeller et al. 2017). These examples highlight the need for more accurate inventory data on wood properties that could facilitate precise forest management decisions made at finer spatial and temporal scales, accounting for both biomass accumulation and wood quality.

1.2.3. *Forest biomass*

Forest biomass is an important source of information on forest carbon stock, sequestration, and wood quantity. Forest biomass at the stand level is inferred from allometric tree biomass estimates (Repola 2009). Similarly, carbon storage and sinks are calculated from the forest biomass, using fixed wood density and carbon content factors (Penman et al. 2003) that are specific to single species or genera. However, wood density varies significantly between and within species and individuals, stands, and geographic regions (Duncanson et al. 2019; Momo et al. 2020; Stephenson et al. 2014).

Existing allometric models that relate tree biomass with tree attributes such as H and diameter-at-breast height (DBH) do not comprehensively describe the differences between different developmental stages, forest types, or canopy positions, and require frequent calibration when conditions change. The problem is associated with the generally low transferability of the current species-specific biomass models between geographical regions

(Duncanson et al. 2015; Duncanson et al. 2019). More transferable results could be obtained, using additional crown metrics in the allometric equations and volume-weighted wood density factors in volume-to-biomass conversion (Kankare et al. 2013; Momo et al. 2018). Moreover, significant uncertainties also remain in the forecasts of future forest growth and carbon uptake that are based on process-based, dynamic vegetation models, one of the reasons being the lack of explicit description of wood formation processes in the models (Friend et al. 2019).

1.2.4. Wood quality

Wood quality, in terms of superiority and inferiority, refers to human perceptions and is dependent on the intended use of wood. In general, wood quality refers to the mechanical properties of end products, e.g. timber stiffness, strength, durability, stability, and appearance, or pulp stiffness, coarseness, and density (Moore and Cown 2015). Here, I focus mainly on wood quality in timber (i.e. timber quality). Timber quality is predominantly influenced by wood density, *MFA*, knots, and grain orientation. Consequently, visual strength grading of sawn wood is based on measures of ring width, knots, grain straightness, and occurrences of decay, reaction wood, and other anomalies that affect important wood properties. Similarly, sawlogs are graded and sorted prior to sawing according to their dimensions, appearance, and, increasingly, measurements of wood density and knottiness based on x-ray tomography (or digital radiography) at sawmills (Oja et al. 2003).

The unknown variability in wood quality introduces uncertainty that increases the costs of production (Hurtta et al. 2017; Kangas et al. 2012). Primarily, the predictability of quality in both the raw material input and final product output is desirable. Information on wood quality could reduce the amount of wood needed for harvesting and storage at factory yards. Secondarily, the separation of highest quality raw material from the bulk to be used for specialty products is an attractive option for increasing the value-added of wood.

Wood quality estimations of standing timber would be a useful means for more precise planning of forest management and wood procurement. However, actual applications are still sparse, due to the lack of suitable methods for measuring wood quality indicators in the forested environment. Wood quality indicators are morphological tree traits that are used either as direct proxies of a certain property of wood or end product, or as inputs into grading systems or statistical models that predict wood properties and quality. Some of the most common stem and crown metrics used as wood quality indicators include:

- *DBH*, *H* and sawlog (or stem) volume (V_{sawlog}) are common forest inventory attributes for tree size, and related to the maturity of wood and the percentage of structural timber.
- Stem taper, i.e. the rate at which the stem diameter changes as the function of height (also expressed in terms of slenderness, or conicality) is related to growth rate, EW:LW ratio, and maturity of wood (Lindström 1996).
- Stem sweep/stem straightness, i.e. the deviation of the stem from a straight line, affects usability in sawing and may indicate reaction wood content and grain orientation (Rune and Warensjö 2002; Warensjö and Rune 2004).
- H_{lc} is closely related to the maturation of wood (Kuprevicius et al. 2013; Mansfield et al. 2007).
- H_{db} indicates the percentage of clear stem wood at the base of the stem (Uusitalo 1997).

- Whorl-to-whorl distances reflect the primary growth (shoot elongation), with varying implications for ring width, EW content, knottiness, and maturity of wood (Kucera 1994; Mäkinen 1998).
- Maximum branch diameter (*MBD*) indicates the overall knottiness of wood (Björklund and Petersson 1999).
- Branch diameters and insertion angles indicate the knottiness of wood, stem growth rate, and grain orientation (Björklund 1997; Moberg 2006).
- Varying ratios between the above-mentioned indicators (e.g. DBH/H , H_c/H , $Taper/DBH$) indicate tree allometry, i.e. growth allocation between tree parts, maturation of wood, and the resulting wood properties (Kuprevicius et al. 2013).

In addition, more arbitrary factors such as occurrences of abiotic and biotic damage caused by drought, frost, wind, fungus, and insects (often simultaneously or adjacently coupled) or mechanical damage during harvesting, hauling, and storage may also affect wood quality. However, they are beyond the scope of this thesis.

Various grading systems have been developed to sort and distribute the harvestable or harvested timber according to the most suitable end use. For example, studies lasting several decades in Finland aimed at determining the value relationships of different logs with respect to the expected quality of the timber produced (Heiskanen and Siimes 1959; Kärkkäinen 1980; Vuoristo 1937). These systems presented two to three diameter classes and three to five log or tree quality grades, based on observations of select wood quality indicators, e.g. branches, stem shape, visible defects, and stem diameters. An application of the system presented by Kärkkäinen (1980) is practiced to a certain extent in the National Forest Inventory in Finland. Later systems presented empirical and process-based simulation models to predict the distributions of various sawn wood products and their quality grades (Lyhykäinen et al. 2009; Uusitalo 1997). State-of-the-art sawmills utilize sawing simulators that optimize sawing patterns for specific batches of logs. The simulations use virtual sawlogs produced from the sawmill databases of optical and x-ray-based sorting information (Auty et al. 2014a; Lemieux et al. 2000; Todoroki 1990), or from process-based models (Ikonen et al. 2003; Mäkelä et al. 2010; Mäkelä and Mäkinen 2003).

However, none of the systems are effective in operational wood procurement, due to the lack of suitable field references that would otherwise describe wood quality indicators in sufficiently high detail and accuracy (Ojansuu et al. 2018). The wood quality indicators listed above can be used to estimate many key wood properties when used as descriptors of wood formation (Figure 1). Models for predicting wood properties from the characteristics of standing timber could be used to provide additional information not directly obtainable from log dimensions and to produce virtual sawlogs for more flexible definitions of grading rules and optimization of the bucking and sawing patterns (Mäkelä et al. 2010; Mäkinen et al. 2020). Their inclusion in future remote-sensing-aided forest management and wood procurement planning could improve the precision of forestry operations and forest use, with possibly positive implications for the sustainability of managed forests.

1.3. Laser scanning of wood properties in forest management and use

1.3.1. Remote sensing of forests and the role of laser scanning

Global monitoring of forest growth, coverage, and structure is predominantly based on the use of remote-sensing-based model inferences. Increasingly, data are collected from various

sensors and platforms, ranging from space- to airborne and terrestrial laser scanners, cameras, and radars (Dong et al. 2003; Réjou-Méchain et al. 2019). For the spatial extents of ecoregions and entire biomes, satellite data are currently the only viable sources. However, airborne and terrestrial laser scanning (ALS and TLS, respectively) are most accurate and effective in acquiring high-resolution structural data locally. These data are then used as groundtruth for satellite-based spatial models (Luther et al. 2019; Puliti et al. 2018; Réjou-Méchain et al. 2019; Saarela et al. 2015).

Laser scanning acquires point-based geometrical and spectral data, using transmitters and receivers that emit laser signals—pulses or continuous waves of compressed light with narrow spectral band width—and record their returning amplitudes (i.e. intensities) and either phase-shift or time-of-flight to calculate the distance the signal traversed. Using the transmission angle of the laser-beam origin and the distance, three-dimensional (3-D) coordinates of points on the object(s) that reflected the laser can be calculated, relative to the scanner location. Increasingly, laser scanning is being performed from multiple complementary aerial and terrestrial platforms to collect structural data from forests at variable resolutions and perspectives (Beland et al. 2019; Lindberg and Holmgren 2017) (Figure 2).

1.3.2. Airborne laser scanning—mapping canopy structures and growth conditions

ALS is used to acquire point clouds over landscapes or local regions from an aeronautical platform, such as an airplane or helicopter. The most commonly available national and commercial ALS data provide 0.5–10 points per m² and 0.15–0.5-m footprints that are dependent on scanning altitude, cruising speed, and pulse frequency. Ground elevations, land-use classes, large infrastructures, and forest canopies are examples of elements that can, ideally, be distinguished. Objects smaller than the footprints are generally indistinguishable. ALS has been used in the Nordic countries for elevation models, mapping, land-use planning, and national forest inventories since the early 21st century. The greatest advantage of ALS for forest inventories is it being an active remote-sensing technique, in contrast to passive remote sensing (photogrammetric, or image-based) (Yu et al. 2015). Laser beams are capable of penetrating the canopy and provide multiple returns (echoes), or full waveforms for each emitted pulse. These data enable building of digital terrain models (DTMs) and digital surface models (DSMs) of the canopy layer and, subsequently, canopy height models (CHMs). CHM suites direct extraction of canopy height, depth, density, and gap fractions as proxies or predictors of several important forest parameters.

Area-based approaches are utilized in wall-to-wall predictions of forest inventory variables in fixed spatial grids (Lefsky et al. 1999; Næsset 2002; White et al. 2013). Area-based approaches can use readily available, sparse ALS data with 0.5–2 points per m². Grid-level point cloud features (e.g. height percentiles, point penetration, gap fractions, intensity features, texture) are empirically linked with inventoried forest attributes (e.g. stand height, basal area (G), growing stock density) from sample plots or other forest inventory sample units.

Previous research conducted on the estimation of wood quality indicators and wood properties at the grid level showed that stand-specific canopy features extracted from ALS predicted stand-level wood quality indicators, such as G , stand height, stand age, and dominant height (H_{dom}) (Coops et al. 2007; Hilker et al. 2012; Maltamo et al. 2009; Racine et al. 2013), wood properties such as wood density, fiber length, and MFA (Hilker et al. 2013; Luther et al. 2014; Pokharel et al. 2016; Wylie et al. 2019) and mechanical properties of

timber (Fischer et al. 2018). However, the transferability of the relationships found has generally been low, which is likely due to the lack of accounts of tree-specific differences, as well as the intra-tree variations in wood properties. Moreover, one of the most stubborn bottlenecks limiting the more detailed use of ALS data is the lack of reliable methods for classifying tree species, especially with complex forest structures (Fassnacht et al. 2016).

The spatial resolution of aerial point cloud data is anticipated to increase, due to the development of single-photon sensor technology (Swatantran et al. 2016; Wästlund et al. 2018) and drones (or unmanned aerial vehicles, UAVs) as platforms (Coops et al. 2019). The remaining technological challenges aside (e.g. oversensitivity of single-photon sensors and legislative problems of UAVs), future use of individual tree delineation (ITD) (Hyypä and Inkinen 1999) could thus become more often feasible. Tree-specific crown features enable more detailed estimations of the most common forest inventory variables and their stand- or grid-specific distributions (Maltamo et al. 2018; Vauhkonen et al. 2009; Wang et al. 2016). ITD-based studies on predicting tree-specific wood quality indicators have shown more robust relationships under variable stand conditions (Korhonen et al. 2019).

However, the research is still inconclusive as to how features of individual trees delineated from ALS should be used to predict various wood properties. Moreover, to take further advantage of single-tree resolution, forest inventories should also collect more detailed field references on tree morphologies and forest structures with spatial information that could be linked with their respective ITD segments. Ground-based laser-scanning systems are seen as potential solutions to develop the level of detail in field references.

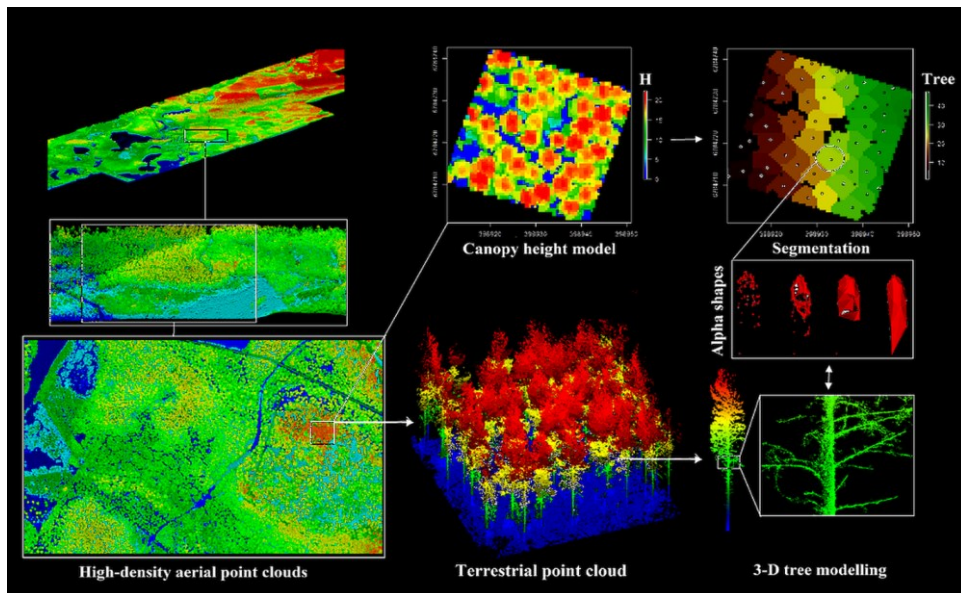


Figure 2. Examples of terrestrial and airborne point clouds available for forest inventories. Dense aerial point clouds facilitate mapping of individual tree crowns over landscapes, while terrestrial point clouds provide detailed three-dimensional (3-D) morphological tree parameters at the sample plot level. Establishment of predictive models between wood quality indicators resolved from terrestrial point clouds and crown features from aerial point clouds (based on alpha shapes, for example) could be used to extrapolate the wood quality indicators over landscapes and estimate wood properties in individual stems. Figure partially adapted from article V.

1.3.3. Terrestrial laser scanning—detailed geometrical models of tree morphologies

TLS refers to laser scanning performed on ground-level platforms that are usually static, e.g. tripods (Jupp and Lovell 2007; Liang et al. 2016; Maas et al. 2008). Mobile laser scanning (MLS) is distinguished from TLS to emphasize the mobility of the sensor platform, e.g. backpack, all-terrain vehicle, car, or harvester (Kukko et al. 2012; Liang et al. 2018b). These methods provide dense and detailed point clouds of the surroundings, but with relatively short spatial range. Typical point-to-point sampling distances vary around a few millimeters over a 10-m distance, with footprints below 1 cm. Depending on the forest type, the point density per square meter can be several tens of thousands, while the operative range for TLS where tree stems are recorded at least partly is usually around 15–30 m. Generally, TLS and MLS point clouds oversample the ground and the lower parts of stems and canopies, but become dramatically sparser higher in the crown as scanner distance and occlusion increase. Stochastic noise is often present, mostly due to background radiation (e.g. sunlight), backscattering caused by air moisture or dust, and beams that have illuminated several objects or irregular planes (Forsman et al. 2018). Although using multiple vantage points can increase the coverage and range as well as the point cloud density in upper canopies, TLS is best suited for data acquisition at the sample plot level, or on individual trees (Abegg et al. 2017; Beland et al. 2019; Liang et al. 2018a; Saarinen et al. 2017; Wilkes et al. 2017).

MLS could enable more efficient collection of data over areas larger than that reasonably covered by TLS, but severe inaccuracy remains in the coregistration of points into a common coordinate system when the lengths of sub-canopy MLS trajectories increase (Kaartinen et al. 2015). Most recently, low-altitude or intra-canopy UAVs have enabled data acquisition in the higher parts of tree stems and crowns that could possibly be used to complement the data from terrestrial sensors (Liang et al. 2019). While operationally functional MLS and UAV-based laser-scanning systems are under development, TLS remains one of the most precise systems for use in a forested environment and is a viable tool for researching future point cloud-based forestry applications.

Point cloud features similar to those used with ALS (e.g. point-based and intensity-based) can be used to describe stand attributes (Jupp et al. 2009) and even model wood properties at stand-level scale (Blanchette et al. 2015). However, an increasing number of studies have investigated the applicability of TLS point clouds to geometrical tree modeling, using quantitative approaches that would enable highly automated retrieval of tree structures in a forested environment (Bournez et al. 2017; Bucksch and Lindenbergh 2008; Côté et al. 2011; Gorte and Pfeifer 2004; Hackenberg et al. 2014; Hancock et al. 2017; Liang et al. 2012; Olofsson et al. 2014; Pfeifer et al. 2004; Raunonen et al. 2013; Yrttimaa et al. 2019). In the extraction and reconstruction of tree parts from terrestrial point cloud data, four main steps are generally involved:

1. Filtering: denoising, homogenizing, and down-sampling of the point cloud
 - a. Stray points removed, based on the spatial neighborhood
 - b. Noisy points removed, based on intensity
 - c. Point density homogenized, using fixed-size voxels, or other methods
 - d. Voxel, or point space reduced to octrees, k -d trees, or other more efficient data structures
 - e. (Point intensities normalized if intensity/spectral information is used)
2. Classifying: labeling points belonging to ground, tree stems, branches, and foliage
 - a. Grid-based and triangulation methods, based on point distances

- b. Clustering methods, based on the spatial distribution of points, using area-growing algorithms, or hierarchical clustering
 - c. Geometrical methods, based on the dimensionality of points in spatial neighborhoods, using principal component analysis (PCA) or machine learning
 - d. Classification methods, based on point intensity or spectral information
- 3. Structuring: Identifying individual stems and branches and ordering them into hierarchical tree structures
 - a. Tree skeleton methods
 - b. Connectivity analyses
 - c. Pattern recognition, using iterative pattern matching or machine learning
- 4. Modeling: characterizing tree parts geometrically
 - a. Triangulation or interpolation methods for surface fitting (convex hulls, alpha shapes)
 - b. Fitting of geometrical primitives (cylinders, circles), using least-squares or maximum-likelihood approximation, often enhanced with iteration, e.g. random sample consensus (RANSAC)

Thus, a great variety of options and different techniques are available for use in each of the phases, including varying combinations of them. Moreover, steps may be performed in differing order, simultaneously or repeatedly. In addition, statistical smoothing approaches to filter the outcome (e.g. stem curves or the vertical distribution of branch diameters) is often required after the actual geometrical modeling (Saarinen et al. 2017). TLS observations can also be treated as inputs to process-based tree architectural models to overcome gaps in point clouds (Côté et al. 2011; Côté et al. 2018). The choices are dependent upon the data used and outcome sought. Increasingly detailed and complex 3-D descriptions of tree structures have been used for a multitude of applications that could be useful in the estimation of wood properties:

- Direct estimation of tree volumes throughout tree compartments and their conversion to biomass estimates (Calders et al. 2015; Hackenberg et al. 2015)
- Calibration of allometric tree volume or growth equations (both empirical and process-based) (Côté et al. 2018; Saarinen et al. 2017; Stovall et al. 2017)
- Retrieval of tree-specific wood quality indicators (Höwler et al. 2017; Kankare et al. 2014; Kretschmer et al. 2013; Stängle et al. 2014; Thies et al. 2004)
- Tree species identification, based on tree morphology (Åkerblom et al. 2017)
- Analyses of forest canopy space occupation and competition (Bayer et al. 2013; Hess et al. 2018; Metz et al. 2013; Su et al. 2020)
- Estimating the distribution of photosynthetically active radiation within and below the canopies (Cifuentes et al. 2017; Côté et al. 2009)
- Estimations of architecture-based metabolic scaling exponents (Lau et al. 2019)

However, the number of studies is still relatively small, and several questions remain considering the optimal use of TLS and other terrestrial point clouds in the estimation of wood properties. More information is required regarding the accuracy and performance of point clouds and algorithms used to retrieve tree morphology. Challenges associated with the coverage, density, and accuracy of the point clouds are directly transformed to errors in reconstructed tree parts. Optimal sampling schemes for acquiring data representative of the variability in stem and crown geometries within a forest area likewise remain unclear.

1.4. Thesis scope and objectives

The aim here was to determine how wood properties could be estimated in remote-sensing-based forest inventories. The aim entailed increasing the understanding of the feasibilities and challenges associated with data acquisition, processing, modeling, and applications. In addition, sharing information between the two disciplines involved was addressed: informing the remote-sensing community of the relevant theoretical background of wood formation as well as wood technologists of the availability and technological feasibilities and limitations of remote-sensing methods to assess wood properties.

In the original articles (I–V), methods for characterizing wood quality indicators in standing timber were developed and examined from the perspective of the technical feasibilities of the remote-sensing technologies, algorithms, sampling schemes, and modeling methods selected for capturing relevant tree structures over multiple scales. The point-of-view in the original articles was mostly focused on wood procurement and forest use, i.e. the utilization of the technologies examined to improve conditions in the forest industry to target harvests more precisely, and to promote sustainable use of wood. The implications for forest management decisions and biomass estimations in forests are considered, as well.

The reader should also be advised that the scope of this thesis (and the original articles) was exclusively focused on Scots pine (*Pinus sylvestris* L.) in intensively managed, even-aged, single-species boreal forests on mineral soils. The wood properties targeted (e.g. knottiness and wood density) were analyzed, using select wood quality indicators, i.e. descriptors of stem, crown size, and structure, and the accuracies directly assessed with x-ray references from sawmills when available, or implicitly with respect to the theoretical background of wood formation as described. High-resolution remote-sensing methods were used (TLS and ALS) that are not yet available in operational forest inventorying. With these considerations in place, the objectives of the thesis were:

1. To identify wood quality indicators that can be captured, using TLS, and to assess their accuracy (I–IV).
2. To assess the accuracy of ALS crown features for predicting TLS-based wood quality indicators throughout the landscape (V).
3. To analyze how the retrievable indicators could be used to model wood properties and wood quality in remote-sensing-based forest inventories (I–V).
4. To infer the implications for enhanced forest management and use (I–V).

2. MATERIALS AND METHODS

2.1. Study areas, sample trees, and plots

The study areas comprised Scots pine-dominated, even-aged managed boreal forest stands on mineral soils located in southern Finland in Evo, Orimattila, and Hyytiälä. The stands examined represented one of the major sources of softwood timber in southern Finland.

We used data for 180 mature Scots pines sampled from six different forest stands in Evo (4) and Orimattila (2), 30 trees per each stand, located in groups of 2–10 trees (Table) (I–III). The stands were selected to represent mature Scots pine stands under various forest conditions in terms of site fertility and thinning intensity. The trees were sampled to represent

the diameter distributions of each stand. We collected TLS data of the standing timber and x-ray scanning data of the sawlog sections harvested at the Koskitukki sawmill (Koskitukki Oyj, Järvelä, Finland).

We used data for 52 Scots pines from a single mature stand in Hyytiälä (Table) (IV). The trees were selected to represent the diameter distribution of the stands, located in 10 groups of 2–6 trees. We acquired TLS data of the standing timber, and optical and x-ray data of the sawlogs harvested and bucked at Korkeakoski Sawmill (UPM-Kymmene Oyj, Korkeakoski, Finland).

We used data from 27 Scots pine stands in Evo (V). The stands examined were selected to document the transition of Scots pine stands from young to mature developmental stages, and thus a spectrum of varying wood quality indicators in the area. In all, 24 sample plots were established at representative locations, one in each stand. In addition, we placed four plots in each of three remaining stands that captured the main stages of the transition. TLS data and tree-specific field measurements were collected from all sample plots (36).

2.2. Reference data

2.2.1. Field measurements

Field measurements were carried out with typical measurement gear deployed in current operational stand-wise forest inventories in Finland. Stem size and height are the most commonly used of the forest inventory attributes that are also used as the ground-truth for remote-sensing-based predictions. In addition, we inspected select crown size variables that are used in more specific inventories.

The field references were collected for each sample tree, using calipers and a digital hypsometer Vertex III (Haglöfs AB, Järfälla, Sweden) (I–III). DBH was measured with the calipers as an average of two perpendicular measurements of the stem diameter at 1.3-m height from the ground. H , H_{db} , and H_{lc} were measured with the Vertex, using an average of three repetitions; H was the height of the treetop from the ground, H_{db} was the height of the lowest dead branch from the ground, and H_{lc} was the height of the lowest living branch that was separated from the live crown by a maximum of one dead whorl.

In article IV, no field references were collected.

A field crew obtained the field references for all individual trees within the plots of 32×32 m that exceeded a 5-cm DBH (V). The field crew used a preliminary tree map to locate all trees within the plot borders, identified the species for each tree, and measured DBH , H , H_{db} , and H_{lc} , similar to those noted elsewhere (I, II, and IV). In addition, trees missing from the tree maps were added, using a measuring tape and a bearing compass to define the locations.

2.2.2. Sawmill measurements

Sawmill measurements were undertaken at sawmills, using the operational measurement systems including optical and x-ray scanning devices. In x-ray scanning, we focused on knottiness and wood density, since these wood properties were considered some of the most pivotal to wood quality, and x-raying companies have established methods for their extraction. Operational x-ray scanning at sawmills is based on x-ray densitometry, in which the intensities of x-rays transmitted through the logs are used to reconstruct a digital, two-dimensional (2-D) gray-scale image for linear interpretation of wood density (with respect to

device-specific calibration measurements), and varying means of pattern recognition to distinguish whorls of knots (Wei et al. 2011). Among other issues, rapid processing, uneven moistness of the logs, and the limited number of x-raying directions limit the accuracy of wood property features extracted from x-ray scanning, but nevertheless represent the state-of-the-art wood property information achievable at industrial scale.

Sawmill references were obtained for the log-sections of each sample tree at Koskitukki Oy with an Opmes AX1 (Inray Oy Ltd, Mikkeli, Finland) x-ray scanning device (or digital radiographer) (I). The scanning was performed successfully for 162 of the 180 trees. The data included the vertical locations of all whorls and the maximum knot diameter in each whorl.

Sawmill references were collected from the sawlogs bucked from the sample trees at Korkeakoski Sawmill (IV). We obtained data from the optical log-scanner system Visiometric LignaProfi (Visiolog Ltd., Lappeenranta, Finland) and the x-ray scanning system Wood-X 4D Tomo (Finnos Oy, Lappeenranta, Finland) used operationally at the sawmill. The data included stem geometry variables (stem dimensions, stem taper, and stem sweep) and wood property variables of knottiness and wood density.

2.3. Study data

2.3.1. Terrestrial laser-scanning data acquisition and preprocessing

TLS data were collected from groups of sample trees and sample plots with an aim at capturing the relevant morphological traits used for estimating wood properties and wood quality. These traits (stem geometry and branching structures) were considered as complete as possible, given the limitations imposed by the forested environment, e.g. occlusion and wind.

TLS data were collected for the tree groups from variable scanning positions adjusted specifically for each group to ensure full coverage on all sides of all trees in the group (I–III). We used a Faro Focus^{3D} X 330 phase-shift scanner (Faro Technologies Inc., Lake Mary, FL, USA). The point-to-point sampling distance was set to 6.3 mm at a 10-m distance, resulting in 44.4 M points measured.

TLS data were obtained with similar adjusted scanning setups, using a Trimble TX5 (Trimble Inc., Sunnyvale, CA, USA) phase-shift scanner, with point-to-point sampling distance set to 3.1 mm at a 10 distance, resulting in 177.7 M points measured (IV). The TLS data were obtained from the sample plots, using five scanner locations that were fixed to all plots, namely in the center of the plot and in the center of each plot quadrant (V). We used either of the two scanners: the Focus^{3D} or a Leica HDS6100 (Leica Geosystems AG, Heerbrugg, Switzerland). With both scanners, the point-to-point sampling distance was set to 6.3 mm at a 10-m distance.

In all scanning setups, six target spheres were placed within the scanned area, such that all six were visible to at least one of the scans, and at least three spheres were visible to all other scans. The global coordinates of the spheres were also measured, using a Trimble R8 real-time kinematic Global Navigation Satellite System (GNSS) receiver and a Trimble 5602 DR200+ total station (V).

Similar preprocessing procedures were used in all TLS datasets utilizing the built-in preprocessing algorithms in the software according to the scanner manufacturer. Faro Scene 5.2 was used for the Focus^{3D} and TX5 data and Leica Z+F LaserControl 8.6 for the HDS6100 data.

We removed the stochastic noise by filtering out spatial and spectral outliers, e.g. points that had no neighbors within a 3x3 pixel 2-D grid in Faro Scene and points that had too low a return intensity (below 300 in Faro Scene on a scale of 0–2096). Typically, up to half of the points in the original point cloud were filtered out at this stage.

We co-registered the separate scans from a group of trees or a sample plot into a common coordinate system, using the target sphere locations to solve the positions and orientations of scans relative to each other.

2.3.2. *Terrestrial laser-scanning point cloud-based geometrical tree-modeling methods*

Individual trees were handled separately to digitize the stems and branching for the extraction of wood quality indicators. Both manual and quantitative (or automated) methods were used to reconstruct stems and first-order branches.

In I, tree stems and the largest first-order branches in diameter within each whorl were manually digitized from the sample tree point clouds and reconstructed, using RANSAC circle fitting (Fischler and Bolles 1981). H_{ab} was estimated from the TLS data as the height of the lowest detected branch (or whorl).

In II and III, the sample trees were manually extracted from the point clouds. Geometrical tree stem and branch reconstructions were quantitatively produced from the point clouds, using point cloud classification, pattern recognition, and fitting of geometrical primitives (circles and cylinders): we carried out PCA for 3-D point neighborhoods and classified the points as stem, branch, and noisy points, based on their orientation and flatness (Liang et al. 2012). We modeled the stem by fitting consecutive cylinders to the stem points from the tree bottom to top. For branch detection, the stem model was split into vertical segments 15 cm in height at 5-cm intervals, i.e. 15-cm consecutive segments with a 10-cm vertical overlap. The distribution of branch points in each vertical segment as a function of degrees around the stem was smoothed by a convolution with a Gaussian window function. Branches were identified from the smoothed function, using a continuous wavelet-transform peak-detection method (Du et al. 2006). The branch points detected were modeled, utilizing RANSAC circle fitting.

In IV, the sample trees were manually extracted, and the stems were quantitatively reconstructed, using the classification and cylinder-fitting procedure developed by Liang et al. (2012).

In V, the sample trees were extracted from the sample plot-level point clouds, based on the segmentation of the TLS CHMs produced for each plot. A sample of the extracted trees was selected from each plot and the stem and branching reconstructed, using the methods described elsewhere (II and III).

2.3.3. *Airborne laser-scanning data acquisition, feature extraction, selection, and modeling*

In V, we acquired ALS data that covered the entire Evo study area (app. 2000 hectares) with pulse density suitable for ITD. The scanner used was a Leica ALS70-HA. The data were collected from an altitude of 900 m above sea level, and the resulting data showed an average pulse density of six pulses per m² with a footprint of 13.5 cm. The system recorded a maximum of five echoes per pulse.

We produced DTMs and DSMs of the upper canopy, and by subtracting DTM from DSM, generated normalized CHMs of the sample plots. ITD on CHMs was carried out, using an iterative local maxima-based watershed algorithm. For all delineated tree crowns, several

point-based and geometrical (using alpha-shapes (Edelsbrunner and Mücke 1994)) features were calculated, in addition to which competition and stand descriptors were derived from the crown features, based on neighborhood- and plot-level calculations, respectively (see V, Table 2 for an exhaustive list).

The best subsets of all extracted features for predicting each of the wood quality indicators were selected separately for each response variable, using regression trees (Breiman et al. 1984). Variables found decisive in the splitting nodes of the regression trees were selected as explanatory variables in the prediction models.

The prediction models were built, using the Random Forest (RF) machine learning algorithm (Breiman 2001). RF builds ‘forests’ of regression trees from random subsamples of the modeling data, and randomly permutes explanatory variables at each splitting node. The final prediction was based on a regression tree averaged from all random-generated regression trees.

2.4. Statistical analyses

Evaluations were based on the analyses of descriptive statistics, using paired t-tests, mean difference (MD, or mean error ME, or bias), root-mean-squared error (RMSE), Pearson’s correlation coefficients (r), and coefficient of determination (R^2) to assess the accuracy of the methods examined with respect to their references. The feasibilities of the TLS data, the quantitative methods applied and the ALS modeling scheme to capture tree traits that could be used to assess various wood properties were inferred from the results.

In I, we evaluated the accuracy of the TLS multi-scan point clouds in capturing the branching structures in standing timber in comparison to those measured with operational sawmill equipment, using paired t-tests.

In II, we evaluated the performance of the quantitative branch detection and modeling method developed in direct comparison to the manual measurements from article I. In other words, the optimal performance of the algorithm was assessed with respect to the observable branching structures, given the point cloud completeness. We defined the accuracy of whorl detection, based on the number of correct false-positive (commission error) and false-negative (omission error) observations. We compared the accuracy of the branch diameter and insertion angle estimates in terms of bias and RMSE.

In III we analyzed the performance of the quantitative branch detection algorithm across five vertical stem sections. Samples of branches were randomly selected from each stem section and manual measurements compared with the quantitative similar to the comparisons in II. We used multiple regression models to assess the effects of scanner distance and occlusion on the performance of our branch detection and modeling methods.

In IV, we assessed the accuracy of the TLS stem models in comparison to the sawmill data, using paired t-tests at the log level, and analyzed the relationships of the log geometry with wood density and knottness, using Pearson’s correlation coefficients.

In V, we determined the accuracy of the ALS features in predicting TLS-based tree-specific wood quality indicators with RF (V). We calculated ME, RMSE, R^2 between the TLS-derived values and the RF-predicted values. The coverage and representativeness of our sampling and prediction schemes were also analyzed, based on probability density functions and hierarchical cluster analyses of the wood quality indicators predicted.

The Materials and methods are summarized in Table 1.

Table 1. Summary of materials and methods in original articles I-V. *DBH* is diameter-at-breast height, *H_{db}* is height of the lowest dead branch, RMSE is root-mean-squared error, *R*² is coefficient of determination, MD is mean difference, ME is mean error, ITD is individual tree delineation, RF is Random Forest, RANSAC is Random Sample Consensus, TLS is terrestrial laser scanning, ALS is airborne laser scanning.

	Wood quality indicators	Study material and area	Study data ----- References	Sampling	Methods	Statistical analysis
I	<i>DBH</i> , <i>H_{db}</i> , number of whorls, whorl-to-whorl distances	Six mature Scots pine stands (mineral soil, even-aged) Evo, Orimattila, Myrskylä (southern Finland)	Manual TLS measurements ----- X-ray & field measurements	180 trees representing the diameter distribution. Largest branch in each whorl within log sections (stem diameter >15 cm)	Visual interpretation, RANSAC circle fitting	Comparison of descriptive statistics; paired t-tests
II	Number of whorls, branch diameter, branch insertion angle	Six mature Scots pine stands (mineral soil, even-aged) Evo, Orimattila, Myrskylä (southern Finland)	Quantitative TLS features ----- Manual TLS measurements	180 trees representing the diameter distribution. Largest branch in each whorl within log sections (stem diameter >15 cm)	Quantitative branch detection and modeling: continuous wavelet-transform-based pattern recognition	Accuracy analysis and comparison of descriptive statistics; bias, RMSE
III	Number of whorls, branch diameter, branch insertion angle	Six mature Scots pine stands (mineral soil, even-aged) Evo, Orimattila, Myrskylä (southern Finland)	Quantitative TLS features ----- Manual TLS measurements	180 trees representing the diameter distribution. All branches in 1-m samples in 5 stratified stem sections from every tree	Quantitative branch detection and modeling: continuous wavelet-transform-based pattern recognition	Accuracy analysis, and simple & multiple linear regression models; bias, <i>R</i> ²
IV	Stem dimensions and shape	One mature Scots pine stand (mineral soil, even-aged) Hyytiälä (southern Finland)	TLS stem models ----- Optical log scanner, X-ray	52 randomly sampled trees. Log sections (stem diameter >15 cm) bucked to bottom, middle, and top log	Quantitative stem modeling: stem point classification and cylinder fitting	Comparison of descriptive statistics; MD, paired t-tests, Pearson's correlations

Table 1. (Continues)

	Wood quality indicators	Study material	Study data ----- References	Sampling	Methods	Statistical analysis
V	Stem and crown dimensions	27 Scots pine stands from young to mature (mineral soil, even-aged) Evo (southern Finland)	ALS crown features and TLS modeling data ----- Quantitative TLS features & field measurements	10% of trees in each sample plot representing the diameter distribution	Quantitative stem and branch modeling; extraction of wood quality indicators from TLS point clouds. ITD, and the extraction of crown features from ALS point clouds. Nonparametrical feature selection (regression trees), iterative resampling and model predictions (RF)	Comparisons of observed (TLS and field) and predicted values; ME, RMSE, R^2 . Analysis of sample and prediction representativeness; probability density functions and hierarchical cluster analysis

3. RESULTS AND DISCUSSION

3.1. Summary of the results in the original articles

In I, we observed that the main differences between branching structures captured by TLS and x-ray scanning resulted from self-pruned branches in the lower parts of the log sections. However, the $MBDs$ in the TLS data did not differ from those in the x-ray data with statistical significance. H_{db} was measured from TLS with an ~ 1 -m MD compared with the field measurements. We concluded that the stem dimensions and visible branches in the lower dead parts of the crown were recorded reliably in the point clouds (Table 2). Quantitative (or automated) extraction of useful wood quality indicators from point clouds was identified as the next crucial development step.

In II and III we found that the quantitative branch detection and modeling method developed specifically for our purposes was a reliable means to describe the first-order branching (i.e. branches deviating from the main stem) within dead crowns (Figure 3). A tree-specific average of 69.9% of the whorls in the log sections was observed (II), compared with the number of whorls visually identifiable from the point clouds. In all, 68.8% of the visually identified branches were found with the quantitative approach, when inspecting vertically stratified samples (III). The quantitative detection accuracy decreased dramatically above H_{lc} , due to increasing scanner distance and decreasing point density. Wind and occlusion showed additional adverse effects on detection and modeling accuracy. The method also generally resulted in underestimation of the branch diameters, compared with the manual point cloud measurements of the branches. In all, our results suggested that full branching structures cannot be captured by TLS alone, but the retrievable parameters could be treated as inputs to allometric branching models and used for tree biomass and wood quality estimation (Table 2).

In IV, we found that stem dimensions resolved from the TLS point clouds compared favorably with those measured by state-of-the-art sawmill equipment (Figure 3) (IV). The stem dimensions also exhibited logical relationships with wood properties, such as knottiness and wood density; however, the correlations remained moderate ($r < 0.5$). Sweep estimation from the TLS point clouds did not coincide with the sawmill measurements, possibly due to the use of different measurement principles. TLS accounted for the 3-D shapes of the stems, while the sawmill measurements relied on 2-D stem profiles. In addition, the sweeping may have been greater in the standing timber, due to the gravity of branches and foliage on upright stems, as opposed to bucked and pruned logs laid horizontally. Nevertheless, our results supported our idea that wood property models built from sawmill databases (i.e. models that related log geometry with interior wood properties) could be applied to standing timber, using stem variables measured with TLS (Table 2). In an operational setting, point cloud data could likely be more effectively collected by means of MLS (e.g. from a harvester).

In V, we obtained reliable RF predictions for TLS-derived DBH , V_{sawlog} , and H_{lc} , using the ALS point cloud features ($R^2 > 0.4$), while more detailed branching attributes (MBD and H_{db}) could not be directly modeled from the ALS features (Table 2). Based on the regression tree analysis, tree-specific ALS point height features, geometrical proxies for crown size, and stand-specific point height features were the most abundant descriptors of wood quality indicators. In our data, H_{lc} , as predicted from the crown features, enabled distinguishing between mature Scots pine stands better than stem size alone. In general, RF predictions for DBH in low and high extremes were more averaged than those of H_{lc} . We concluded that accounting for individual tree crown features in ALS-based forest inventories could enable more detailed descriptions of tree morphologies and inferences of their effects on stem growth and wood quality.

Table 2. Summary of descriptive results in the assessment of wood quality indicator variables in the original articles, with respective conclusions. DBH is diameter-at-breast height, V_{sawlog} is volume of the sawlog section, H_{lc} is the live crown base height, H_{db} is height of the lowest dead branch, and MBD is the maximum branch diameter. Estimates derived from the terrestrial laser-scanning (TLS) point cloud subscripted with 'TLS', and Random Forest predictions based on airborne laser-scanning (ALS) features with 'RF'. Sawmill measurements are subscripted with 'sawmill'. Field-measured variables have no subscript. MD and ME are mean difference and mean error, respectively. RMSE is root-mean-squared error.

Variable	Evaluations of results (I–V)	Conclusions
DBH	I: $DBH_{TLS} - DBH$	MD 0.69 cm (2.2%)
	V: $DBH_{TLS} - DBH$	ME -0.38 cm (-1.8%)
		RMSE 1.42 cm (6.9%)
	$DBH_{RF} - DBH_{TLS}$	ME -0.07 cm (-0.4%)
		RMSE 2.70 cm (13.3%)
V_{sawlog}	IV: $V_{sawlogTLS} - V_{sawlogSawmill}$	MD -0.004 m3 (-2.42%)
	V: $V_{sawlogTLS} - V_{sawlog}$	ME -0.060 m3 (-17.8%)
		RMSE 0.10 m3 (30.8%)
	$V_{sawlogRF} - V_{sawlogTLS}$	ME -0.002 m3 (-0.7%)
		RMSE 0.11 m3 (41.2%)

Table 2. (Continues)

Variable	Evaluations of results (I–V)	Conclusions
Taper	IV: $Taper_{TLS} - Taper_{sawmill}$ MD -0.24 mm/m (-2.98%)	Taper can be estimated directly from the TLS stem curve. Taper affects the sawing pattern and correlates moderately with select wood properties (e.g. knottiness and wood density).
Sweep	IV: $Sweep_{TLS} - Sweep_{sawmill}$ MD 3.50 mm/m (78.13%)	Sweep can be measured from the TLS stem curve, but the measurements were not compatible with those at the sawmill. Sweep affects the optimal log breakdown and is linked with reaction wood and grain straightness.
H_{lc}	V: $H_{lcTLS} - H_{lc}$ $H_{lcRF} - H_{lcTLS}$ ME 0.96 m (8.6%) RMSE 2.39 m (21.5%) ME -0.02 m (-0.2%) RMSE 1.89 m (15.7%)	H_{lc} can be estimated from the TLS point cloud, using the distribution of branch diameters, and is predictable from the ALS features. H_{lc} is an important indicator of crown vigor and maturity of wood.
H_{db}	I: $H_{dbTLS} - H_{db}$ V: $H_{dbTLS} - H_{db}$ $H_{dbRF} - H_{dbTLS}$ MD 0.80 m (14.2%) ME 0.80 m (19.8%) RMSE 1.94 m (47.9%) ME 0.04 m (0.8%) RMSE 1.89 m (15.7%)	H_{db} can be estimated from the TLS point clouds as the height of the lowest branch, but cannot easily be predicted with the ALS features. H_{db} is an indicator of the clearwood content at the base of the stem.
MBD	I: $MBD_{TLS} - MBD_{sawmill}$ V: $MBD_{TLS} - MBD$ $MBD_{RF} - MBD_{TLS}$ MD 0.42 mm (1.81%) ME 1.90 mm (5.6%) RMSE 7.40 mm (22.0%) ME -0.10 mm (-0.2%) RMSE 6.10 mm (17.1%)	MBD can be measured from the TLS point clouds, but the accuracy is dependent on the point cloud density. MBD is not directly predictable from the ALS features. MBD is the single most important indicator of knottiness and crown vigor. MBD can also be empirically predicted from stem and crown allometry.
Whorls	I: TLS - Sawmill Mean whorl height MD -1.56 m Whorl number MD -14.07 (37.7%) Whorl-to-whorl distance MD 0.11 m (34.3%) II: Manual - Quantitative (TLS) Number of whorls Accuracy 71.1%	Whorls are distinguishable in dead crowns, using the TLS point clouds. Self-pruned whorls and those in live crowns cannot be measured. The vertical distribution of whorls is a useful indicator of crown structure and height increments and relates to the earlywood content and maturation of wood.
Branching	I: TLS - Sawmill Mean branch diameter MD 0.65 cm (28.0%) II: Manual - Quantitative (TLS) Branch diameter Bias 0.32 cm (9.2%) RMSE 1.92 cm (61.7%) Branch insertion angle Bias 0.55° (0.6%) RMSE 15.91° (24.5%) III: Manual - Quantitative (TLS) Number of branches Accuracy 68.6% Branch diameter Bias 0.89 cm (40.3%) RMSE 0.94 cm (42.5%) Branch insertion angle Bias 1.98° (3.1%) RMSE 7.75° (12.0%)	Branch diameters and angles can be measured for dead branches, using TLS. Point cloud density highly affects the detection accuracy. The vertical distribution of the branching parameters could be used to build or calibrate allometric branching functions, however the representativeness would be poor in higher parts of live crown. Nevertheless, branching parameters can serve various purposes in the modelling of wood properties.

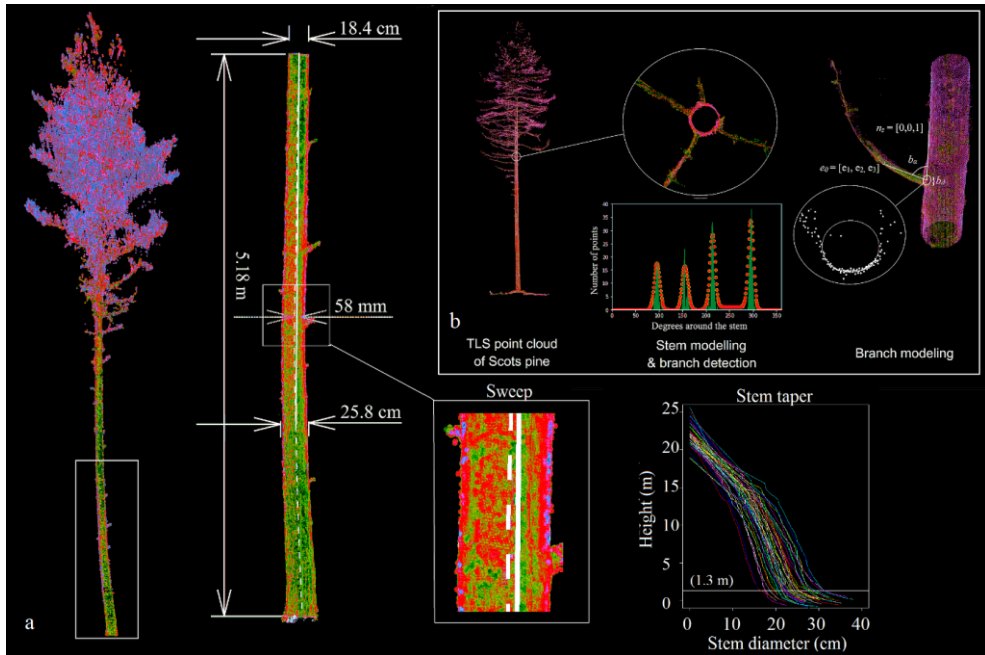


Figure 3. Examples of terrestrial laser-scanning (TLS) point clouds and retrievable wood quality indicators. (a) The lower parts (log sections) of the stems are distinguishable from the point clouds. The stem dimensions and shape (e.g. sweep and vertical stem taper) can be extracted from geometrically reconstructed stems. (b) The individual branches can be detected with favorable accuracy within the dead crowns of the log-sized trees. The branch diameters and branch insertion angles are estimated, e.g. with circle fitting and principal component analysis, respectively. The accuracy of the wood quality indicators retrieved was dependent largely on point cloud quality, coverage, and density. The best results were obtained with TLS point clouds of individual sample trees or small groups of trees, as opposed to those of larger sample plots. Adapted from articles II and IV.

3.2. Methodological considerations and restrictions

The sample sizes used in the original articles were small. Therefore, the reader should bear in mind that the scope was on a particular tree species (1), forest conditions (2), wood properties (3), morphological tree traits (4), and remote-sensing methods (5):

- 1) The thesis focused exclusively on **Scots pine**. Although softwoods share a variety of similarities, considering their wood properties, the predominant sources of differences should be borne in mind: Scots pine is a shade-intolerant species with plastic crown structure, thus strongly responsive to the environment and variable in wood quality. Other softwood species and genera exhibit different types of shade tolerance, crown plasticity, and growth responses, with different implications for wood properties.
- 2) The thesis focused on **even-aged, Scots pine-dominated managed forests on mineral soils in southern Finland**, i.e. in a region strictly restricted in geography, climate, and ecology. The variability of Scots pine wood properties under selected conditions is

generally well-known, which enabled logical analyses of our results with respect to the theoretical background. In addition, the structural homogeneity of the forest conditions examined was considered to isolate the effect of data acquisition considerations. However, although similar management options in comparable soils are commonly used with a variety of *Pinus* species globally, the results presented here cannot be held as representative of other species, ecoregions, or uneven-aged or mixed forests, or forests on peatlands.

- 3) The thesis focused on the properties of the vascular xylems in Scots pine—such as **knottiness**, **MFA**, and **wood density**—that are theoretically characterizable through the tree morphology. Reaction and opposite wood, or anomalies of wood (e.g. wound tissues and decay) that affect the wood properties targeted were not considered in the thesis. Both direct and implicit assessments of wood properties were used:
 - a. Direct wood property measurements were carried out, using state-of-the-art x-ray scanning at sawmills, which has its own limitations: the high processor speed limits the accuracy of x-rays, as well as the number of computable features. Wood moisture may bias the density measurements among logs, especially in sapwood. The limited number of measurement directions may cause occlusion of knots and decay, and overlapping features may bias the measurements. The x-ray scanning used in this thesis should not be confused with 3-D x-ray computed tomography scanning (Wei et al. 2011).
 - b. The implicit inferences of knottiness, *MFA*, and wood density were justified, based on their known responses to growth and the environment. These wood properties have high narrow-sense heritability by definition, i.e. the variance of the relevant genetic responses is considered *additive* to the predominant environmental effects and to cause relatively little variation in these properties (Zobel and Jett 2012).
- 4) Simple tree attributes such as *DBH*, *H_{db}*, *H_{lc}*, and *MBD* were used as the descriptors of **tree morphology**. These variables were considered to cover the most important morphological traits associated with the development of the selected wood properties in managed Scots pine stands. The variables were inferred from stem and branching data that could also enable more detailed description of the tree structures, e.g. stem dimensions and shape as well as branch diameters and insertion angles as functions of height. However, the complexity of wood formation implies that the variability in wood properties throughout the various scales will always be greater than that of the wood quality indicators, i.e. wood formation processes cannot be completely explained by stem and branching attributes.
- 5) **High-density TLS and ALS 3-D point clouds** were used in the thesis and represented remote-sensing data not (yet) deployed in operational forest inventory regimes. Therefore, all results entail hypothetic (or futuristic) settings, where the prevailing bottlenecks in data acquisition and computation are in most parts solved. More specifically:
 - a. TLS data was used to characterize sample trees and plots. In the absence of operational settings for gathering detailed 3-D point cloud data in the forested environment (e.g. MLS from harvesters), TLS is currently considered one of the most accurate methods applicable to research purposes. TLS represents the potential accuracy of the data achievable from terrestrial platforms (i.e. taking into account the inevitable effects of wind, occlusion, and reducing of point density by the scanner distance).

- b. ALS data with the resolution of app. six points per m² gathered from an altitude of 900 m were used for the spatial modeling (V). The bulk of the contemporary aerial 3-D remote-sensing data have lower resolution than these. However, the development of new sensors (e.g. single-photon technology, high-resolution satellite imagery) and platforms (e.g. drones) can be anticipated to increase the spatial resolution of future aerial remote-sensing data.
- c. The data-processing methods were considered representative of the currently available methods, excluding the remaining computational limitations and unknown performance outside the particular study material. The efficiency, accuracy, and availability of various algorithms and required computing power were not exhaustively considered in the thesis, and they are expected to continue improving from those presented here.

For the above reasons, the small sample sizes used in the original articles were considered adequate for the explorative purposes of the thesis—demonstrations of highly detailed methods were given at the expense of robustness and transferability. Generalizations outside this particular material must be avoided.

Our settling for small samples can in part be attributed to the limitations of data acquisition. TLS point cloud coverage quickly diminished with increasing scanner distance, thus limiting the operative range to individual sample trees or sample plots, and the metrics obtainable to the lower canopy and stems, especially with quantitative methods (Abegg et al. 2017; Liang et al. 2018a; Maas et al. 2008; Wilkes et al. 2017). Larger sample sizes could be obtained with MLS, if not for the prevailing inaccuracies in data registration that still limit the extents of feasible data (Liang et al. 2018b).

In our data, the accuracy of several wood quality indicators differed between datasets with different point densities (Table 2). For example, V_{sawlog} was estimated with high accuracy, using dense point clouds collected from small groups of mature sample trees (IV) (MD -2.42% in comparison to sawmill measurements). Similar estimates were found less accurate when derived from point clouds of plots sized 32x32 m with lower point density (V) (ME -17.8% in comparison to volume calculations based on an existing allometric function) (Table 2).

ITD-based ALS point cloud features enabled predictions of the main morphological tree traits that are required as inputs to wood property and wood quality models within a landscape. The main restrictions affecting the feasibility of ITD-based tree trait estimation include challenges in species recognition and retrieval of data from lower canopy layers (Chasmer et al. 2006; Korpela et al. 2010; Wang et al. 2016). These aspects require further development, especially for enabling application of the methods examined to more heterogeneous forests.

3.3. Applications in the modeling of wood properties and wood quality

The TLS point clouds were feasible means for recording select tree morphologies relevant to wood quality in intensively managed Scots pine stands. The estimates in our studies were mostly concise, with measurements carried out in the field with conventional tools, as well as in sawmills with state-of-the-art optical and x-ray-based equipment. Simple dependencies were identified between stem and branching parameters obtainable from TLS and tree-specific wood property statistics such as *MBD*, mean whorl-to-whorl distance, and mean wood density measured with x-rays.

The results suggest that TLS should be considered as a tool for retrieving input variables to allometric wood property or wood quality models. Data should be obtained from a carefully selected sample of trees that represents the variability of wood properties in the area (or population) of interest. For example, an analysis by Saarinen et al. (2019) showed that a relatively small sample of representative individuals is enough to reparameterize an empirical stem taper function for a well-defined population.

Tree growth models (empirical or process-based) describe the relationships of primary and secondary growth as allometries between H , stem and crown dimensions, branching, and volume and biomass partitioning (Achim et al. 2006; Groot and Schneider 2011; Houllier et al. 1995; Kellomäki et al. 1999; Laasasenaho 1982; Mäkelä 1986; Mäkinen and Colin 1998). The tight interdependencies between primary and secondary growth are due to the wood formation responding to intrinsic (increasing size) and extrinsic (climate and competition) factors as described in the Introduction. With detailed inputs from TLS point clouds accompanied by wood property references, any of the above-mentioned models could be utilized in translating allometric growth responses into vertical and radial gradients of wood properties such as knottiness, wood density, or fiber properties (Duchateau et al. 2013; Eberhardt et al. 2019; Ikonen et al. 2003; Mäkelä et al. 2010; Mäkinen et al. 2020; Moberg 2006; Osborne and Maguire 2016) (Figures 1 and 4).

The full facilitation of methods such as those examined in this thesis should aim at upscaling wood properties from the tree-ring level to global extent, utilizing increased communication between various disciplines, such as remote sensing, wood science, forest ecology, dendrochronology, and other environmental sciences (Babst et al. 2018; Beland et al. 2019). The underlying complexity of wood formation processes remains only fragmentally described from cellular scales to annual rings and whole-tree level to forest stands, regions, and forest biomes (Babst et al. 2018; Friend et al. 2019). The findings in this thesis suggest that high-density terrestrial and aerial remote-sensing methods can play an important role in filling in the knowledge gaps regarding wood property variabilities throughout different spatial extents, from intra-tree processes and stand dynamics to geographical regions and climatic gradients.

Wood quality models could utilize detailed terrestrial point cloud data in multiple ways. One option would include MLS performed from harvesters during forest operations and linking point cloud measurements with industrial data. Establishing databases that combine detailed morphological tree traits from standing timber, bucking data from harvesters, and wood quality data from sawmills would enable reconstructions of virtual sawlogs that are used to optimize the secondary log breakdown, or sawing. Using stem taper, branching, and knot shape models, comprehensive reconstructions of interior knot structures were previously demonstrated (Duchateau et al. 2013; Osborne and Maguire 2016). TLS provides an excellent instrument for obtaining the calibration data from standing timber (Figure 4). The virtual sawlogs should be compatible with sawing simulators that are used at sawmills to choose optimal sawing patterns for specific batches of logs and to estimate product recoveries with wood quality information (Auty et al. 2014a; Ikonen et al. 2003). Promisingly, Murphy et al. (2010) already used TLS stem models as inputs to an optimization program that accounted for optimal bucking and sawing, based on stem size and shape.

If virtual sawlogs were imputed to standing timber prior to harvesting (Figure 4), very accurate and timely optimization of wood procurement could be practiced. Positioning data from scanners and harvesters should therefore be preserved along the sawmill's process chain to enable links to remote-sensing sources (at least at the stand level) (Karttinen et al. 2015; Saukkola et al. 2019). Models for predicting bucking, log-specific wood quality, or optimal

log breakdown at the individual tree level could be extrapolated over the stands of interest, using remote sensing if the data (e.g. ALS) enabled the predictions of sufficient input variables. Similar approaches were already demonstrated with harvester data, field measurements, and aerial remote-sensing data (Barth et al. 2015; Sanz et al. 2018). Already the inclusion of H_{lc} in the suite of variables inventoried with ALS, as also proposed by other authors (Korhonen et al. 2019; Maltamo et al. 2018), would open way for a wide range of allometric wood property models that could be applied.

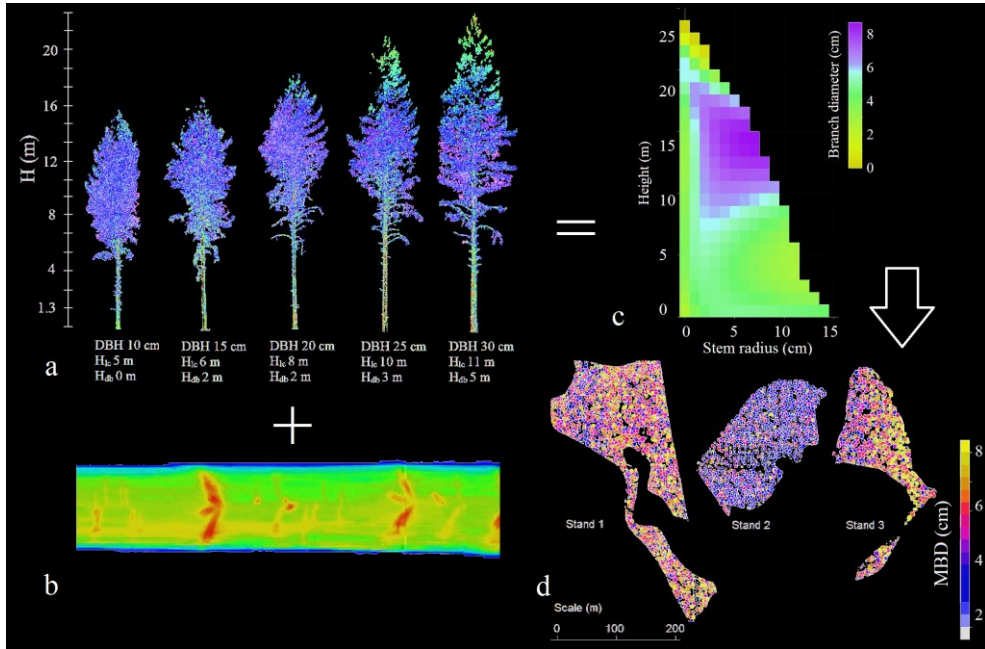


Figure 4. Outlook for utilizing high-resolution terrestrial point clouds, sawmill references, and aerial point clouds to estimate wood properties in standing timber. (a) Terrestrial point clouds enable measurements of detailed stem and branching parameters from standing timber. (b) State-of-the-art x-ray log tomography equipment at sawmills measure whorl locations and wood density (adapted from article IV, by courtesy of Finnos Oy). (c) Coupling terrestrial point clouds with sawmill data could enable modeling of wood property gradients within stems. (d) Dense airborne laser-scanning data can be used to map wood properties to individual tree segments, based on wood quality indicators predicted from the point cloud features. In this example, tree-specific maximum branch diameters (MBDs) were predicted, using crown features and calibrated branching models (unpublished work). DBH is the diameter-at-breast height.

3.4. Implications for forest management and use

The uncertainty of future climates and environments coupled with the increased demand for wood introduces new challenges to forest management and use. Most importantly, more precise and flexible planning of forest management and wood procurement are needed to ensure the productivity of forests as well as the maintenance of sufficient wood supply (Gardiner and Moore 2014). The approaches examined in this thesis could be parts of more precise future forest planning. The ability to calibrate wood property and wood quality

models according to the target area or population characteristics could improve the accuracy of carbon sequestration and timber production estimations across forest types, developmental stages, and geographical regions. It should further be determined whether more detailed wood property information could be used to facilitate forestry policies that promote improvements in wood quality through silviculture and wood markets that benefit from this improved quality (Hurtta et al. 2017).

Intensive forest management practices with short rotations have long been held in their part responsible for the decline in wood quality in industrially harvested wood (Zobel 1984). Delayed harvests (or prolonged rotations) could improve the wood quality in managed forests and increase the percentage of mature wood and structural timber in the wood harvested. Unfortunately, extending the rotations is controversial, due to the slow increase in net-value in old trees, and because the largest trees are often the most vulnerable to the threats posed by changing climate, such as drought, unusual wind conditions, spreading diseases, and insect outbreaks (Bennett et al. 2015). In the current volume-centric markets, trees are harvested when the proportional annual increase in the price gained for the accumulated volume is lower than the reference interest rate. Ideally, if wood markets used wood quality-based sale premiums, forest owners could be encouraged to delay their harvests (Malinen et al. 2010). Prolonged rotations should be accompanied by the major portion of wood being turned into long-term carbon-binding sawn wood.

Managed forests in many regions of temperate and tropical forests are under the threat of forest degradation or deforestation, due to the reduced forest biodiversity and, consequently, lower resistance, resilience, and productive stability (Hosonuma et al. 2012). Boreal forests could face similar threats as climate change proceeds (Gauthier et al. 2015). One of the most pivotal questions in contemporary silvicultural science is how forest management could improve the conditions for forests to be adaptable to future changes. It is arguable that future forest management should be planned at notably finer spatial and temporal resolutions to increase the flexibility of forest management and use. The variability in wood quality is thus likely to become more nuanced between trees and stands, highlighting the need for more accurate remote-sensing-aided wood property and wood quality estimation methods, such as those studied in this thesis.

4. CONCLUSIONS

Ongoing changes in climate, environment, silviculture, and demand for wood are creating pressure for more precise forest management and use, key components of which are spatially and temporally explicit models of wood properties. Wood properties (e.g. tracheid dimensions, wood density, *MFA*) are pivotal to the accumulation of biomass in forests and the quality of wood in various end uses, especially in structural timber. Explicit and spatially transferable models for describing wood properties and wood quality are required to enable precise monitoring of wood formation in forests and planning of sustainable forest management and wood procurement. Remote sensing holds significant promise for introducing such implementations into practice, especially due to the recent emergence of terrestrial point clouds and increasingly dense ALS data.

The most common inputs to a variety of wood property and wood quality models are descriptors of stem and branching. In this thesis, we found that TLS was capable of recording the relevant structures in high detail, but within small spatial ranges. Simple wood quality indicators were also successfully modeled, using ALS-based crown features. However, the more explicit branching attributes were found challenging to predict directly from ALS

features. The representativeness and coverage of sampling, as well as data quality and accuracy, were of great importance to the feasibilities of the methods.

Based on the results of this thesis, TLS should be considered as a tool for retrieving stem and branching data from sample trees and for building or calibrating allometric models (empirical or process-based) of explicit stem and branching structures. Several wood properties, and the resulting biomass and wood quality, can be inferred from such morphological reconstructions by utilizing the dependencies between primary and secondary growth (e.g. EW to LW and juvenile to mature wood transitioning). Linking detailed morphological tree measurements from TLS with sawmill data would enable highly accurate wood procurement planning with accounts for wood quality. Wood property and wood quality models should use tree traits predictable with ALS as explanatory variables (e.g. *H*, crown dimensions).

More frequent interdisciplinary communication would be beneficial in further research. With an understanding of the ecological background of wood formation, remote-sensing data would enable modeling frameworks for various wood properties that have been previously elusive to the forest inventories. On the other hand, the increasing access to morphological modeling data could improve the feasibility of wood scientific applications in sustainable forest management and use. Such developments should become increasingly useful in tackling the challenges associated with changing environment, climate, silviculture, and demand for wood.

REFERENCES

- Abegg, M., Kükenbrink, D., Zell, J., Schaepman, M. E. & Morsdorf, F. (2017). Terrestrial Laser Scanning for Forest Inventories—Tree Diameter Distribution and Scanner Location Impact on Occlusion. *Forests*, 8(6), 184. <https://doi.org/10.3390/f8060184>
- Achim, A., Gardiner, B., Leban, J. & Daquitaine, R. (2006). Predicting the Branching Properties of Sitka Spruce Grown in Great Britain. *New Zealand Journal of Forestry Science*, 36(2/3), 246.
- Åkerblom, M., Raunonen, P., Mäkipää, R. & Kaasalainen, M. (2017). Automatic Tree Species Recognition with Quantitative Structure Models. *Remote Sensing of Environment*, 191, 1-12. <https://doi.org/10.1016/j.rse.2016.12.002>
- Amarasekara, H. & Denne, M. (2002). Effects of Crown Size on Wood Characteristics of Corsican Pine in Relation to Definitions of Juvenile Wood, Crown Formed Wood and Core Wood. *Forestry*, 75(1), 51-61. <https://doi.org/10.1093/forestry/75.1.51>
- Anon (2019). "Wood". Merriam-Webster.com. [31.10.2019]
- Arneth, A., Sitch, S., Pongratz, J., Stocker, B. D., Ciais, P., Poulter, B., Bayer, A. D., Bondeau, A., Calle, L., Chini, L. P., Gasser, T., Fader, M., Friedlingstein, P., Kato, E., Li, W., Lindeskog, M., Nabel, J. E. M. S., Pugh, T. a. M., Robertson, E., Viovy, N., Yue, C. & Zaehle, S. (2017). Historical Carbon Dioxide Emissions Caused by Land-Use Changes Are Possibly Larger Than Assumed. *Nature Geoscience*, 10(2), 79. <https://doi.org/10.1038/Ngeo2882>

- Auty, D., Achim, A., Bédard, P. & Pothier, D. (2014a). Statsaw: Modelling Lumber Product Assortment Using Zero-Inflated Poisson Regression. *Canadian Journal of Forest Research*, 44(6), 638-647. <https://doi.org/10.1139/cjfr-2013-0500>
- Auty, D., Achim, A., Macdonald, E., Cameron, A. D. & Gardiner, B. A. (2014b). Models for Predicting Wood Density Variation in Scots Pine. *Forestry: An International Journal of Forest Research*, 87(3), 449-458. <https://doi.org/10.1093/forestry/cpu005>
- Auty, D., Moore, J., Achim, A., Lyon, A., Mochan, S. & Gardiner, B. (2018). Effects of Early Respacing on the Density and Microfibril Angle of Sitka Spruce Wood. *Forestry: An International Journal of Forest Research*, 91(3), 307-319. <https://doi.org/10.1093/forestry/cpx004>
- Babst, F., Bodesheim, P., Charney, N., Friend, A. D., Girardin, M. P., Klesse, S., Moore, D. J. P., Seftigen, K., Bjorklund, J., Bouriaud, O., Dawson, A., Derosé, R. J., Dietze, M. C., Eckes, A. H., Enquist, B., Frank, D. C., Mahecha, M. D., Poulter, B., Record, S., Trouet, V., Turton, R. H., Zhang, Z. & Evans, M. E. K. (2018). When Tree Rings Go Global: Challenges and Opportunities for Retro- and Prospective Insight. *Quaternary Science Reviews*, 197, 1-20. <https://doi.org/10.1016/j.quascirev.2018.07.009>
- Babst, F., Bouriaud, O., Poulter, B., Trouet, V., Girardin, M. P. & Frank, D. C. (2019). Twentieth Century Redistribution in Climatic Drivers of Global Tree Growth. *Science advances*, 5(1), eaat4313. <https://doi.org/10.1126/sciadv.aat4313>
- Barth, A., Möller, J. J., Wilhelmsson, L., Arlinger, J., Hedberg, R. & Söderman, U. (2015). A Swedish Case Study on the Prediction of Detailed Product Recovery from Individual Stem Profiles Based on Airborne Laser Scanning. *Annals of forest science*, 72(1), 47-56. <https://doi.org/10.1007/s13595-014-0400-6>
- Bayer, D., Seifert, S. & Pretzsch, H. (2013). Structural Crown Properties of Norway Spruce (*Picea Abies* [L.] Karst.) and European Beech (*Fagus Sylvatica* [L.]) in Mixed Versus Pure Stands Revealed by Terrestrial Laser Scanning. *Trees*, 27(4), 1035-1047. <https://doi.org/10.1007/s00468-013-0854-4>
- Begum, S., Nakaba, S., Yamagishi, Y., Oribe, Y. & Funada, R. (2013). Regulation of Cambial Activity in Relation to Environmental Conditions: Understanding the Role of Temperature in Wood Formation of Trees. *Physiologia Plantarum*, 147(1), 46-54. <https://doi.org/10.1111/j.1399-3054.2012.01663.x>
- Beland, M., Parker, G., Sparrow, B., Harding, D., Chasmer, L., Phinn, S., Antonarakis, A. & Strahler, A. (2019). On Promoting the Use of Lidar Systems in Forest Ecosystem Research. *Forest Ecology and Management*, 450, 117484. <https://doi.org/10.1016/j.foreco.2019.117484>
- Benjamin, J. G., Kershaw, J., John A, Weiskittel, A. R., Chui, Y. H. & Zhang, S. (2009). External Knot Size and Frequency in Black Spruce Trees from an Initial Spacing Trial in Thunder Bay, Ontario. *Forestry Chronicle*, 85(4), 618-624. <https://doi.org/10.5558/tfc85618-4>

Bennett, A. C., McDowell, N. G., Allen, C. D. & Anderson-Teixeira, K. J. (2015). Larger Trees Suffer Most During Drought in Forests Worldwide. *Nature Plants*, 1(10), 15139. <https://doi.org/10.1038/Nplants.2015.139>

Björklund, J., Seftigen, K., Schweingruber, F., Fonti, P., Von Arx, G., Bryukhanova, M. V., Cuny, H. E., Carrer, M., Castagneri, D. & Frank, D. C. (2017). Cell Size and Wall Dimensions Drive Distinct Variability of Earlywood and Latewood Density in Northern Hemisphere Conifers. *New Phytologist*, 216(3), 728-740. <https://doi.org/10.1111/nph.14639>

Björklund, L. (1997). The Interior Knot Structure of *Pinus Sylvestris* Stems. *Scandinavian Journal of Forest Research*, 12(4), 403-412. <https://doi.org/10.1080/02827589709355429>

Björklund, L. & Petersson, H. (1999). Predicting Knot Diameter of *Pinus Sylvestris* in Sweden. *Scandinavian Journal of Forest Research*, 14(4), 376-384. <https://doi.org/10.1080/02827589950152700>

Blanchette, D., Fournier, R. A., Luther, J. E. & Côté, J.-F. (2015). Predicting Wood Fiber Attributes Using Local-Scale Metrics from Terrestrial Lidar Data: A Case Study of Newfoundland Conifer Species. *Forest Ecology and Management*, 347, 116-129. <https://doi.org/10.1016/j.foreco.2015.03.013>

Bonan, G. B. (2008). Forests and Climate Change: Forcings, Feedbacks, and the Climate Benefits of Forests. *Science*, 320(5882), 1444-9. <https://doi.org/10.1126/science.1155121>

Bournez, E., Landes, T., Saudreau, M., Kastendeuch, P. & Najjar, G. (2017). From Tls Point Clouds to 3d Models of Trees: A Comparison of Existing Algorithms for 3d Tree Reconstruction. *ISPRS-International Archives of the Photogrammetry, Remote Sensing and Spatial Information Sciences*, 42(2), 113-120. <https://doi.org/10.5194/isprs-archives-XLII-2-W3-113-2017>

Breiman, L. (2001). Random Forests. *Machine learning*, 45(1), 5-32. <https://doi.org/10.1023/A:1010933404324>

Breiman, L., Friedman, J., Olshen, R. & Stone, C. (1984). *Classification and Regression Trees*, Belmont, California, Wadsworth, International Group.

Bucksch, A. & Lindenbergh, R. (2008). Campino—a Skeletonization Method for Point Cloud Processing. *ISPRS Journal of Photogrammetry and Remote Sensing*, 63(1), 115-127. <https://doi.org/10.1016/j.isprsjprs.2007.10.004>

Burdon, R. D., Kibblewhite, R. P., Walker, J. C., Megraw, R. A., Evans, R. & Cown, D. J. (2004). Juvenile Versus Mature Wood: A New Concept, Orthogonal to Corewood Versus Outerwood, with Special Reference to *Pinus Radiata* and *P. Taeda*. *Forest science*, 50(4), 399-415. <https://doi.org/10.1093/forestscience/50.4.399>

Cabon, A., Fernández-De-Uña, L., Gea-Izquierdo, G., Meinzer, F. C., Woodruff, D. R., Martínez-Vilalta, J. & De Cáceres, M. (2020). Water Potential Control of Turgor-Driven

Tracheid Enlargement in Scots Pine at Its Xeric Distribution Edge. *New Phytologist*, 225, 209-221. <https://doi.org/10.1111/nph.16146>

Calders, K., Newnham, G., Burt, A., Murphy, S., Raunonen, P., Herold, M., Culvenor, D., Avitabile, V., Disney, M. & Armston, J. (2015). Nondestructive Estimates of above-Ground Biomass Using Terrestrial Laser Scanning. *Methods in Ecology and Evolution*, 6(2), 198-208. <https://doi.org/10.1111/2041-210X.12301>

Canadell, J. G. & Raupach, M. R. (2008). Managing Forests for Climate Change Mitigation. *Science*, 320, 1456-7. <https://doi.org/10.1126/science.1155458>

Cardinale, B. J., Duffy, J. E., Gonzalez, A., Hooper, D. U., Perrings, C., Venail, P., Narwani, A., Mace, G. M., Tilman, D., Wardle, D. A., Kinzig, A. P., Daily, G. C., Loreau, M., Grace, J. B., Larigauderie, A., Srivastava, D. S. & Naeem, S. (2012). Biodiversity Loss and Its Impact on Humanity. *Nature*, 486, 59-67. <https://doi.org/10.1038/nature11148>

Chasmer, L., Hopkinson, C. & Treitz, P. (2006). Investigating Laser Pulse Penetration through a Conifer Canopy by Integrating Airborne and Terrestrial Lidar. *Canadian Journal of Remote Sensing*, 32(2), 116-125. <https://doi.org/10.5589/m06-011>

Cifuentes, R., Van Der Zande, D., Salas-Eljatib, C., Tits, L., Farifteh, J. & Coppin, P. (2017). Modeling 3d Canopy Structure and Transmitted Par Using Terrestrial Lidar. *Canadian Journal of Remote Sensing*, 43(2), 124-139. <https://doi.org/10.1080/07038992.2017.1286937>

Coops, N. C., Goodbody, T. R. & Cao, L. (2019). Four Steps to Extend Drone Use in Research. *Nature*. <https://doi.org/10.1038/d41586-019-02474-y>

Coops, N. C., Hilker, T., Wulder, M. A., St-Onge, B., Newnham, G., Siggins, A. & Trofymow, J. T. (2007). Estimating Canopy Structure of Douglas-Fir Forest Stands from Discrete-Return Lidar. *Trees*, 21(3), 295. <https://doi.org/10.1007/s00468-006-0119-6>

Cortini, F., Groot, A. & Filipescu, C. N. (2013). Models of the Longitudinal Distribution of Ring Area as a Function of Tree and Stand Attributes for Four Major Canadian Conifers. *Annals of Forest Science*, 70(6), 637-648. <https://doi.org/10.1007/s13595-013-0305-9>

Côté, J.-F., Fournier, R. A. & Egli, R. (2011). An Architectural Model of Trees to Estimate Forest Structural Attributes Using Terrestrial Lidar. *Environmental Modelling & Software*, 26(6), 761-777. <https://doi.org/10.1016/j.envsoft.2010.12.008>

Côté, J.-F., Fournier, R. A., Luther, J. E. & Van Lier, O. R. (2018). Fine-Scale Three-Dimensional Modeling of Boreal Forest Plots to Improve Forest Characterization with Remote Sensing. *Remote Sensing of Environment*, 219, 99-114. <https://doi.org/10.1016/j.rse.2018.09.026>

Côté, J.-F., Widlowski, J.-L., Fournier, R. A. & Verstraete, M. M. (2009). The Structural and Radiative Consistency of Three-Dimensional Tree Reconstructions from Terrestrial

Lidar. Remote Sensing of Environment, 113(5), 1067-1081. <https://doi.org/10.1016/j.rse.2009.01.017>

Cuny, H. E., Rathgeber, C. B., Frank, D., Fonti, P., Makinen, H., Prislan, P., Rossi, S., Del Castillo, E. M., Campelo, F., Vavrcik, H., Camarero, J. J., Bryukhanova, M. V., Jyske, T., Gricar, J., Gryc, V., De Luis, M., Vieira, J., Cufar, K., Kirdyanov, A. V., Oberhuber, W., Treml, V., Huang, J. G., Li, X., Swidrak, I., Deslauriers, A., Liang, E., Nojd, P., Gruber, A., Nabais, C., Morin, H., Krause, C., King, G. & Fournier, M. (2015). Woody Biomass Production Lags Stem-Girth Increase by over One Month in Coniferous Forests. *Nature Plants*, 1(11), 15160. <https://doi.org/10.1038/nplants.2015.160>

De Rybel, B., Mähönen, A. P., Helariutta, Y. & Weijers, D. (2016). Plant Vascular Development: From Early Specification to Differentiation. *Nature Reviews Molecular Cell Biology*, 17(1), 30. <https://doi.org/10.1038/nrm.2015.6>

Dong, J., Kaufmann, R. K., Myneni, R. B., Tucker, C. J., Kauppi, P. E., Liski, J., Buermann, W., Alexeyev, V. & Hughes, M. K. (2003). Remote Sensing Estimates of Boreal and Temperate Forest Woody Biomass: Carbon Pools, Sources, and Sinks. *Remote Sensing of Environment*, 84(3), 393-410. [https://doi.org/10.1016/S0034-4257\(02\)00130-X](https://doi.org/10.1016/S0034-4257(02)00130-X)

Du, P., Kibbe, W. A. & Lin, S. M. (2006). Improved Peak Detection in Mass Spectrum by Incorporating Continuous Wavelet Transform-Based Pattern Matching. *Bioinformatics*, 22(17), 2059-65. <https://doi.org/10.1093/bioinformatics/btl355>

Duchateau, E., Longuetaud, F., Mothe, F., Ung, C., Auty, D. & Achim, A. (2013). Modelling Knot Morphology as a Function of External Tree and Branch Attributes. *Canadian Journal of Forest Research*, 43(3), 266-277. <https://doi.org/10.1139/cjfr-2012-0365>

Duncanson, L., Armston, J., Disney, M., Avitabile, V., Barbier, N., Calders, K., Carter, S., Chave, J., Herold, M., Crowther, T. W., Falkowski, M., Kellner, J., Labriere, N., Lucas, R., Macbean, N., Mcroberts, R. E., Meyer, V., Næsset, E., Nickeson, J. E. & Williams, M. (2019). The Importance of Consistent Validation of Global Forest Aboveground Biomass Products. *Surveys in Geophysics*, 40(4), 979-999. <https://doi.org/10.1007/s10712-019-09538-8>

Duncanson, L. I., Dubayah, R. O. & Enquist, B. J. (2015). Assessing the General Patterns of Forest Structure: Quantifying Tree and Forest Allometric Scaling Relationships in the United States. *Global Ecology and Biogeography*, 24(12), 1465-1475. <https://doi.org/10.1111/geb.12371>

Eberhardt, T. L., So, C.-L. & Leduc, D. J. (2019). Wood Property Maps Showing Wood Variability in Mature Longleaf Pine: Does Getting Old Change Juvenile Tendencies? *Wood and Fiber Science*, 51(2), 193-208.

Edelsbrunner, H. & Mücke, E. P. (1994). Three-Dimensional Alpha Shapes. *ACM Transactions on Graphics (TOG)*, 13(1), 43-72. <https://doi.org/10.1145/174462.156635>

Fassnacht, F., Latifi, H., Stereńczak, K., Modzelewska, A., Lefsky, M., Waser, L., Straub, C. & Ghosh, A. (2016). Review of Studies on Tree Species Classification from Remotely Sensed Data. *Remote Sensing of Environment*, 186, 64-87. <https://doi.org/10.1016/j.rse.2016.08.013>

Fischer, C., Høibø, O. A., Vestøl, G. I., Hauglin, M., Hansen, E. H. & Gobakken, T. (2018). Predicting Dynamic Modulus of Elasticity of Norway Spruce Structural Timber by Forest Inventory, Airborne Laser Scanning and Harvester-Derived Data. *Scandinavian Journal of Forest Research*, 33(6), 603-612. <https://doi.org/10.1080/02827581.2018.1427790>

Fischler, M. A. & Bolles, R. C. (1981). Random Sample Consensus: A Paradigm for Model Fitting with Applications to Image Analysis and Automated Cartography. *Communications of the ACM*, 24(6), 381-395. <https://doi.org/10.1145/358669.358692>

Foley, J. A., Defries, R., Asner, G. P., Barford, C., Bonan, G., Carpenter, S. R., Chapin, F. S., Coe, M. T., Daily, G. C., Gibbs, H. K., Helkowski, J. H., Holloway, T., Howard, E. A., Kucharik, C. J., Monfreda, C., Patz, J. A., Prentice, I. C., Ramankutty, N. & Snyder, P. K. (2005). Global Consequences of Land Use. *Science*, 309(5734), 570-574. <https://doi.org/10.1126/science.1111772>

Forsman, M., Börlin, N., Olofsson, K., Reese, H. & Holmgren, J. (2018). Bias of Cylinder Diameter Estimation from Ground-Based Laser Scanners with Different Beam Widths: A Simulation Study. *ISPRS Journal of Photogrammetry and Remote Sensing*, 135, 84-92. <https://doi.org/10.1016/j.isprsjprs.2017.11.013>

Friend, A. D., Eckes-Shephard, A. H., Fonti, P., Rademacher, T. T., Rathgeber, C. B., Richardson, A. D. & Turton, R. H. (2019). On the Need to Consider Wood Formation Processes in Global Vegetation Models and a Suggested Approach. *Annals of Forest Science*, 76(2), 49. <https://doi.org/10.1007/s13595-019-0819-x>

Gardiner, B. & Moore, J. (2014). Creating the Wood Supply of the Future. In: Fenning, T. (ed.) *Challenges and Opportunities for the World's Forests in the 21st Century*. Dordrecht, Germany: Springer. https://doi.org/10.1007/978-94-007-7076-8_30

Gauthier, S., Bernier, P., Kuuluvainen, T., Shvidenko, A. & Schepaschenko, D. (2015). Boreal Forest Health and Global Change. *Science*, 349(6250), 819-22. <https://doi.org/10.1126/science.aaa9092>

Gorte, B. & Pfeifer, N. (2004). Structuring Laser-Scanned Trees Using 3d Mathematical Morphology. *International Archives of Photogrammetry and Remote Sensing*, 35(B5), 929-933.

Groot, A. & Schneider, R. (2011). Predicting Maximum Branch Diameter from Crown Dimensions, Stand Characteristics and Tree Species. *Forestry Chronicle*, 87(4), 542-551. <https://doi.org/10.5558/tfc2011-053>

Hackenberg, J., Morhart, C., Sheppard, J., Spiecker, H. & Disney, M. (2014). Highly Accurate Tree Models Derived from Terrestrial Laser Scan Data: A Method Description. *Forests*, 5(5), 1069-1105. <https://doi.org/10.3390/f5051069>

Hackenberg, J., Wassenberg, M., Spiecker, H. & Sun, D. J. (2015). Non Destructive Method for Biomass Prediction Combining Tls Derived Tree Volume and Wood Density. *Forests*, 6(4), 1274-1300. <https://doi.org/10.3390/f6041274>

Hancock, S., Anderson, K., Disney, M. & Gaston, K. J. (2017). Measurement of Fine-Spatial-Resolution 3d Vegetation Structure with Airborne Waveform Lidar: Calibration and Validation with Voxelised Terrestrial Lidar. *Remote Sensing of Environment*, 188, 37-50. <https://doi.org/10.1016/j.rse.2016.10.041>

Heiskanen, V. & Siimes, F. (1959). Tutkimus Mäntysahatukkien LaatuLuokituksesta. Summary: A Study Regarding the Grading of Pine Saw Logs. *Paperi ja Puu*, 41(8), 359-368.

Hess, C., Härdtle, W., Kunz, M., Fichtner, A. & Von Oheimb, G. (2018). A High-Resolution Approach for the Spatiotemporal Analysis of Forest Canopy Space Using Terrestrial Laser Scanning Data. *Ecology and Evolution*, 8(13), 6800-6811. <https://doi.org/10.1002/ece3.4193>

Hilker, T., Coops, N. C., Newnham, G. J., Van Leeuwen, M., Wulder, M. A., Stewart, J. & Culvenor, D. S. (2012). Comparison of Terrestrial and Airborne Lidar in Describing Stand Structure of a Thinned Lodgepole Pine Forest. *Journal of Forestry*, 110(2), 97-104. <https://doi.org/10.5849/jof.11-003>

Hilker, T., Frazer, G. W., Coops, N. C., Wulder, M. A., Newnham, G. J., Stewart, J. D., Van Leeuwen, M. & Culvenor, D. S. (2013). Prediction of Wood Fiber Attributes from Lidar-Derived Forest Canopy Indicators. *Forest Science*, 59(2), 231-242. <https://doi.org/DOI10.5849/forsci.11-074>

Holopainen, M., Vastaranta, M. & Hyypä, J. (2014). Outlook for the Next Generation's Precision Forestry in Finland. *Forests*, 5(7), 1682-1694. <https://doi.org/10.3390/f5071682>

Hosonuma, N., Herold, M., De Sy, V., De Fries, R. S., Brockhaus, M., Verchot, L., Angelsen, A. & Romijn, E. (2012). An Assessment of Deforestation and Forest Degradation Drivers in Developing Countries. *Environmental Research Letters*, 7(4), 044009. <https://doi.org/10.1088/1748-9326/7/4/044009>

Houllier, F., Leban, J.-M. & Colin, F. (1995). Linking Growth Modelling to Timber Quality Assessment for Norway Spruce. *Forest Ecology and Management*, 74(1), 91-102. [https://doi.org/10.1016/0378-1127\(94\)03510-4](https://doi.org/10.1016/0378-1127(94)03510-4)

Höwler, K., Annighöfer, P., Ammer, C. & Seidel, D. (2017). Competition Improves Quality-Related External Stem Characteristics of *Fagus sylvatica*. *Canadian Journal of Forest Research*, 47(12), 1603-1613. <https://doi.org/10.1139/cjfr-2017-0262>

- Huang, J. G., Deslauriers, A. & Rossi, S. (2014). Xylem Formation Can Be Modeled Statistically as a Function of Primary Growth and Cambium Activity. *New Phytologist*, 203(3), 831-841. <https://doi.org/10.1111/nph.12859>
- Hurtta, H., Cao, T. & Valsta, L. (2017). Optimization of Scots Pine (*Pinus Sylvestris*) Management with the Total Net Return from the Value Chain. *Journal of Forest Economics*, 28, 1-11. <https://doi.org/10.1016/j.jfe.2017.04.001>
- Huuskonen, S., Hakala, S., Mäkinen, H., Hynynen, J. & Varmola, M. (2014). Factors Influencing the Branchiness of Young Scots Pine Trees. *Forestry*, 87(2), 257-265. <https://doi.org/10.1093/forestry/cpt057>
- Hyypä, J. & Inkinen, M. (1999). Detecting and Estimating Attributes for Single Trees Using Laser Scanner. *The Photogrammetric Journal of Finland*, 16(2), 27-42.
- Ikonen, V. P., Kellomäki, S. & Peltola, H. (2003). Linking Tree Stem Properties of Scots Pine (*Pinus Sylvestris* L.) to Sawn Timber Properties through Simulated Sawing. *Forest Ecology and Management*, 174(1-3), 251-263. [https://doi.org/10.1016/S0378-1127\(02\)00035-X](https://doi.org/10.1016/S0378-1127(02)00035-X)
- Jonsson, R., Blujdea, V. N., Fiorese, G., Pilli, R., Rinaldi, F., Baranzelli, C. & Camia, A. (2018). Outlook of the European Forest-Based Sector: Forest Growth, Harvest Demand, Wood-Product Markets, and Forest Carbon Dynamics Implications. *iForest-Biogeosciences and Forestry*, 11(2), 315. <https://doi.org/10.3832/for2636-011>
- Jupp, D. L., Culvenor, D., Lovell, J., Newnham, G., Strahler, A. & Woodcock, C. (2009). Estimating Forest Lai Profiles and Structural Parameters Using a Ground-Based Laser Called 'Echidna®'. *Tree physiology*, 29(2), 171-181. <https://doi.org/10.1093/treephys/tpn022>
- Jupp, D. L. & Lovell, J. L. (2007). *Airborne and Ground-Based Lidar Systems for Forest Measurement: Background and Principles*, CSIRO Marine and Atmospheric Research Canberra, ACT. 1921232684.
- Kaartinen, H., Hyypä, J., Vastaranta, M., Kukko, A., Jaakkola, A., Yu, X. W., Pyöralä, J., Liang, X. L., Liu, J. B., Wang, Y. S., Kaijalainen, R., Melkas, T., Holopainen, M. & Hyypä, H. (2015). Accuracy of Kinematic Positioning Using Global Satellite Navigation Systems under Forest Canopies. *Forests*, 6(9), 3218-3236. <https://doi.org/10.3390/f6093218>
- Kangas, A., Hurtta, H., Mäkinen, H. & Lappi, J. (2012). Estimating the Value of Wood Quality Information in Constrained Optimization. *Canadian Journal of Forest Research*, 42(7), 1347-1358. <https://doi.org/10.1139/x2012-072>
- Kankare, V., Holopainen, M., Vastaranta, M., Puttonen, E., Yu, X., Hyypä, J., Vaaja, M., Hyypä, H. & Alho, P. (2013). Individual Tree Biomass Estimation Using Terrestrial Laser Scanning. *ISPRS Journal of Photogrammetry and Remote Sensing*, 75(1), 64-75. <https://doi.org/10.1016/j.isprsjprs.2012.10.003>

Kankare, V., Joensuu, M., Vauhkonen, J., Holopainen, M., Tanhuanpää, T., Vastaranta, M., Hyypä, J., Hyypä, H., Alho, P., Rikala, J. & Sipi, M. (2014). Estimation of the Timber Quality of Scots Pine with Terrestrial Laser Scanning. *Forests*, 5(8), 1879-1895. <https://doi.org/10.3390/f5081879>

Kärkkäinen, M. (1980). Mäntytukkirunkojen Laatuluokitus. Summary: Grading of Pine Sawlog Stems. *Communicationes Instituti Forestalis Fenniae*, 96(5).

Kellomäki, S., Ikonen, V. P., Peltola, H. & Kolstrom, T. (1999). Modelling the Structural Growth of Scots Pine with Implications for Wood Quality. *Ecological Modelling*, 122(1-2), 117-134. [https://doi.org/10.1016/S0304-3800\(99\)00086-1](https://doi.org/10.1016/S0304-3800(99)00086-1)

Korhonen, L., Repola, J., Karjalainen, T., Packalen, P. & Maltamo, M. (2019). Transferability and Calibration of Airborne Laser Scanning Based Mixed-Effects Models to Estimate the Attributes of Sawlog-Sized Scots Pines. *Silva Fennica*, 53(3), 10179. <https://doi.org/10.14214/sf.10179>

Korpela, I., Ørka, H. O., Maltamo, M., Tokola, T. & Hyypä, J. (2010). Tree Species Classification Using Airborne Lidar—Effects of Stand and Tree Parameters, Downsizing of Training Set, Intensity Normalization, and Sensor Type. *Silva Fennica*, 44(2), 319-339.

Kretschmer, U., Kirchner, N., Morhart, C. & Spiecker, H. (2013). A New Approach to Assessing Tree Stem Quality Characteristics Using Terrestrial Laser Scans. *Silva Fennica*, 47(5). <https://doi.org/10.14214/Sf.1071>

Kucera, B. (1994). A Hypothesis Relating Current Annual Height Increment to Juvenile Wood Formation in Norway Spruce. *Wood and Fiber Science*, 26(1), 152-167.

Kukko, A., Kaartinen, H., Hyypä, J. & Chen, Y. (2012). Multiplatform Mobile Laser Scanning: Usability and Performance. *Sensors*, 12(9), 11712-11733. <https://doi.org/10.3390/s120911712>

Kuprevicius, A., Auty, D., Achim, A. & Caspersen, J. P. (2013). Quantifying the Influence of Live Crown Ratio on the Mechanical Properties of Clear Wood. *Forestry*, 86(3), 361-369. <https://doi.org/10.1093/forestry/cpt006>

Laasasenaho, J. (1982). Taper Curve and Volume Functions for Pine, Spruce and Birch, *Metsäntutkimuslaitos*. 9514005899.

Lachenbruch, B., Moore, J. R. & Evans, R. (2011). Radial Variation in Wood Structure and Function in Woody Plants, and Hypotheses for Its Occurrence. Size-and Age-Related Changes in Tree Structure and Function. Dordrecht, Germany: Springer. https://doi.org/10.1007/978-94-007-1242-3_5

Larson, P. R. (1969). Wood Formation and the Concept of Wood Quality. Bulletin No. 74. Yale University: School of Forestry.

Lau, A., Martius, C., Bartholomeus, H., Shenkin, A., Jackson, T., Malhi, Y., Herold, M. & Bentley, L. P. (2019). Estimating Architecture-Based Metabolic Scaling Exponents of Tropical Trees Using Terrestrial Lidar and 3d Modelling. *Forest Ecology and Management*, 439, 132-145. <https://doi.org/10.1016/j.foreco.2019.02.019>

Law, B. E., Hudiburg, T. W., Berner, L. T., Kent, J. J., Buotte, P. C. & Harmon, M. E. (2018). Land Use Strategies to Mitigate Climate Change in Carbon Dense Temperate Forests. *Proceedings of the National Academy of Sciences*, 115(14), 3663-3668. <https://doi.org/10.1073/pnas.1720064115>

Lefsky, M., Harding, D., Parker, G. & Shugart, H. (1999). Lidar Remote Sensing of Forest Canopy and Stand Attributes. *Remote Sens. Environ*, 67, 83-98.

Lemieux, H., Beaudoin, M. & Grondin, F. (2000). A Model for the Sawing and Grading of Lumber According to Knots. *Wood and fiber science*, 32(2), 179-188.

Liang, X., Kankare, V., Hyypä, J., Wang, Y., Kukko, A., Haggrén, H., Yu, X., Kaartinen, H., Jaakkola, A., Guan, F., Holopainen, M. & Vastaranta, M. (2016). Terrestrial Laser Scanning in Forest Inventories. *ISPRS Journal of Photogrammetry and Remote Sensing*, 115(1), 63-77. <https://doi.org/10.1016/j.isprsjprs.2016.01.006>

Liang, X., Kukko, A., Hyypä, J., Lehtomäki, M., Pyörälä, J., Yu, X., Kaartinen, H., Jaakkola, A. & Wang, Y. (2018a). In-Situ Measurements from Mobile Platforms: An Emerging Approach to Address the Old Challenges Associated with Forest Inventories. *ISPRS Journal of Photogrammetry and Remote Sensing*, 143(1), 97-107. <https://doi.org/10.1016/j.isprsjprs.2018.04.019>

Liang, X., Wang, Y., Pyörälä, J., Lehtomäki, M., Yu, X., Kaartinen, H., Kukko, A., Honkavaara, E., Issaoui, A. E. I., Nevalainen, O., Vaaja, M., Virtanen, J.-P., Katoh, M. & Deng, S. (2019). Forest in Situ Observations Using Unmanned Aerial Vehicle as an Alternative of Terrestrial Measurements. *Forest Ecosystems*, 6(1), 20. <https://doi.org/10.1186/s40663-019-0173-3>

Liang, X. L., Hyypä, J., Kaartinen, H., Lehtomäki, M., Pyörälä, J., Pfeifer, N., Holopainen, M., Brolly, G., Pirotti, F., Hackenberg, J., Huang, H. B., Jo, H. W., Katoh, M., Liu, L. X., Mokros, M., Morel, J., Olofsson, K., Poveda-Lopez, J., Trochta, J., Wang, D., Wang, J. H., Xi, Z. X., Yang, B. S., Zheng, G., Kankare, V., Luoma, V., Yu, X. W., Chen, L., Vastaranta, M., Saarinen, N. & Wang, Y. S. (2018b). International Benchmarking of Terrestrial Laser Scanning Approaches for Forest Inventories. *Isprs Journal of Photogrammetry and Remote Sensing*, 144, 137-179. <https://doi.org/10.1016/j.isprsjprs.2018.06.021>

Liang, X. L., Litkey, P., Hyypä, J., Kaartinen, H., Vastaranta, M. & Holopainen, M. (2012). Automatic Stem Mapping Using Single-Scan Terrestrial Laser Scanning. *IEEE Transactions on Geoscience and Remote Sensing*, 50(2), 661-670. <https://doi.org/10.1109/Tgrs.2011.2161613>

Lindberg, E. & Holmgren, J. (2017). Individual Tree Crown Methods for 3d Data from Remote Sensing. *Current Forestry Reports*, 3(1), 19-31. <https://doi.org/10.1007/s40725-017-0051-6>

Lindström, H. (1996). Basic Density of Norway Spruce. Part II. Predicted by Stem Taper, Mean Growth Ring Width, and Factors Related to Crown Development. *Wood and Fiber Science*, 28(2), 240-251.

Lundqvist, S.-O., Seifert, S., Grahm, T., Olsson, L., García-Gil, M. R., Karlsson, B. & Seifert, T. (2018). Age and Weather Effects on between and within Ring Variations of Number, Width and Coarseness of Tracheids and Radial Growth of Young Norway Spruce. *European Journal of Forest Research*, 137(5), 719-743. <https://doi.org/10.1007/s10342-018-1136-x>

Luther, J., Fournier, R., Lier, O. & Bujold, M. (2019). Extending Als-Based Mapping of Forest Attributes with Medium Resolution Satellite and Environmental Data. *Remote Sensing*, 11(9), 1092. <https://doi.org/10.3390/rs11091092>

Luther, J. E., Skinner, R., Fournier, R. A., Van Lier, O. R., Bowers, W. W., Côté, J.-F., Hopkinson, C. & Moulton, T. (2014). Predicting Wood Quantity and Quality Attributes of Balsam Fir and Black Spruce Using Airborne Laser Scanner Data. *Forestry*, 87(2), 313-326. <https://doi.org/10.1093/forestry/cpt039>

Luyssaert, S., Marie, G., Valade, A., Chen, Y.-Y., Djomo, S. N., Ryder, J., Otto, J., Naudts, K., Lansø, A. S. & Ghattas, J. (2018). Trade-Offs in Using European Forests to Meet Climate Objectives. *Nature*, 562(7726), 259. <https://doi.org/10.1038/s41586-018-0577-1>

Lyhykäinen, H. T., Mäkinen, H., Mäkelä, A., Pastila, S., Heikkilä, A. & Usenius, A. (2009). Predicting Lumber Grade and by-Product Yields for Scots Pine Trees. *Forest Ecology and Management*, 258(2), 146-158. <https://doi.org/10.1016/j.foreco.2009.03.054>

Maas, H. G., Bienert, A., Scheller, S. & Keane, E. (2008). Automatic Forest Inventory Parameter Determination from Terrestrial Laser Scanner Data. *International Journal of Remote Sensing*, 29(5), 1579-1593. <https://doi.org/10.1080/01431160701736406>

Macdicken, K., Jonsson, Ö., Piña, L., Maulo, S., Contessa, V., Adikari, Y., Garzuglia, M., Lindquist, E., Reams, G. & D'annunzio, R. (2016). Global Forest Resources Assessment 2015: How Are the World's Forests Changing?, FAO. 9251092834.

Mackenzie, J. & Bruemmer, G. (2009). Enhancing Canada's Forest Fibre. *Forestry Chronicle*, 85(3), 353-354. <https://doi.org/10.5558/tfc85353-3>

Mäkelä, A. (1986). Implications of the Pipe Model-Theory on Dry-Matter Partitioning and Height Growth in Trees. *Journal of Theoretical Biology*, 123(1), 103-120. [https://doi.org/10.1016/S0022-5193\(86\)80238-7](https://doi.org/10.1016/S0022-5193(86)80238-7)

Mäkelä, A., Grace, J., Deckmyn, G., Kantola, A. & Kint, V. (2010). Simulating Wood Quality in Forest Management Models. *Forest systems*, 19, 48-68.

Mäkelä, A. & Mäkinen, H. (2003). Generating 3d Sawlogs with a Process-Based Growth Model. *Forest Ecology and Management*, 184(1-3), 337-354. [https://doi.org/10.1016/S0378-1127\(03\)00152-X](https://doi.org/10.1016/S0378-1127(03)00152-X)

Mäkinen, H. (1998). The Suitability of Height and Radial Increment Variation in *Pinus Sylvestris* (L.) for Expressing Environmental Signals. *Forest Ecology and Management*, 112(1-2), 191-197. [https://doi.org/10.1016/S0378-1127\(98\)00337-5](https://doi.org/10.1016/S0378-1127(98)00337-5)

Mäkinen, H. (1999). Effect of Stand Density on Radial Growth of Branches of Scots Pine in Southern and Central Finland. *Canadian Journal of Forest Research*, 29(8), 1216-1224. <https://doi.org/10.1139/cjfr-29-8-1216>

Mäkinen, H. & Colin, F. (1998). Predicting Branch Angle and Branch Diameter of Scots Pine from Usual Tree Measurements and Stand Structural Information. *Canadian Journal of Forest Research*, 28(11), 1686-1696. <https://doi.org/10.1139/cjfr-28-11-1686>

Mäkinen, H., Korpunen, H., Raatevaara, A., Heikkinen, J., Alatalo, J. & Uusitalo, J. (2020). Predicting Knottiness of Scots Pine Stems for Quality Bucking. *European Journal of Wood and Wood Products*, 78, 143-150. <https://doi.org/10.1007/s00107-019-01476-x>

Malinen, J., Berg, V. & Kilpeläinen, H. (2010). Roundwood Pricing Mechanisms and Their Performance in Scots Pine Roundwood Markets. *Working Papers of the Finnish Forest Research Institute*, 147, 35.

Maltamo, M., Karjalainen, T., Repola, J. & Vauhkonen, J. (2018). Incorporating Tree-and Stand-Level Information on Crown Base Height into Multivariate Forest Management Inventories Based on Airborne Laser Scanning. *Silva Fennica*, 52(3). <https://doi.org/10.14214/sf.10006>

Maltamo, M., Peuhkurinen, J., Malinen, J., Vauhkonen, J., Packalén, P. & Tokola, T. (2009). Predicting Tree Attributes and Quality Characteristics of Scots Pine Using Airborne Laser Scanning Data. *Silva Fennica*, 43(3), 507-521. <https://doi.org/10.14214/sf.203>

Mansfield, S. D., Parish, R., Goudie, J. W., Kang, K.-Y. & Ott, P. (2007). The Effects of Crown Ratio on the Transition from Juvenile to Mature Wood Production in Lodgepole Pine in Western Canada. *Canadian journal of forest research*, 37(8), 1450-1459. <https://doi.org/10.1139/X06-299>

Metz, J., Seidel, D., Schall, P., Scheffer, D., Schulze, E.-D. & Ammer, C. (2013). Crown Modeling by Terrestrial Laser Scanning as an Approach to Assess the Effect of Aboveground Intra-and Interspecific Competition on Tree Growth. *Forest Ecology and Management*, 310, 275-288. <https://doi.org/10.1016/j.foreco.2013.08.014>

Moberg, L. (2006). Predicting Knot Properties of *Picea Abies* and *Pinus Sylvestris* from Generic Tree Descriptors. *Scandinavian Journal of Forest Research*, 21, 48-61. <https://doi.org/10.1080/14004080500487011>

Momo, S. T., Libalah, M. B., Rossi, V., Fonton, N., Mofack, G. I., Kamdem, N. G., Nguetsop, V. F., Sonké, B., Ploton, P. & Barbier, N. (2018). Using Volume-Weighted Average Wood Specific Gravity of Trees Reduces Bias in Aboveground Biomass Predictions from Forest Volume Data. *Forest ecology and management*, 424, 519-528. <https://doi.org/10.1016/j.foreco.2018.04.054>

Momo, S. T., Ploton, P., Martin-Ducup, O., Lehnebach, R., Fortunel, C., Sagang, L. B. T., Boyemba, F., Couteron, P., Fayolle, A., Libalah, M., Loumeto, J., Medjibe, V., Ngomanda, A., Obiang, D., Pelissier, R., Rossi, V., Yongo, O., Collaborators, P., Sonke, B. & Barbier, N. (2020). Leveraging Signatures of Plant Functional Strategies in Wood Density Profiles of African Trees to Correct Mass Estimations from Terrestrial Laser Data. *Sci Rep*, 10(1), 2001. <https://doi.org/10.1038/s41598-020-58733-w>

Moore, J., Achim, A., Lyon, A., Mochan, S. & Gardiner, B. (2009). Effects of Early Re-Spacing on the Physical and Mechanical Properties of Sitka Spruce Structural Timber. *Forest Ecology and Management*, 258(7), 1174-1180. <https://doi.org/10.1016/j.foreco.2009.06.009>

Moore, J. & Cown, D. (2015). Wood Quality Variability—What Is It, What Are the Consequences and What We Can Do About It? *New Zealand Journal of Forestry*, 59(4), 3-9.

Moore, J. R. & Cown, D. J. (2017). Corewood (Juvenile Wood) and Its Impact on Wood Utilisation. *Current Forestry Reports*, 3(2), 107-118. <https://doi.org/10.1007/s40725-017-0055-2>

Murphy, G., Lyons, J., O'shea, M., Mullooly, G., Keane, E. & Devlin, G. (2010). Management Tools for Optimal Allocation of Wood Fibre to Conventional Log and Bio-Energy Markets in Ireland: A Case Study. *European Journal of Forest Research*, 129(6), 1057-1067. <https://doi.org/10.1007/s10342-010-0390-3>

Næsset, E. (2002). Predicting Forest Stand Characteristics with Airborne Scanning Laser Using a Practical Two-Stage Procedure and Field Data. *Remote Sensing of Environment*, 80(1), 88-99. [https://doi.org/10.1016/S0034-4257\(01\)00290-5](https://doi.org/10.1016/S0034-4257(01)00290-5)

Oja, J., Wallbäcks, L., Grundberg, S., Hägerdal, E. & Grönlund, A. (2003). Automatic Grading of Scots Pine (*Pinus Sylvestris* L.) Sawlogs Using an Industrial X-Ray Log Scanner. *Computers and electronics in agriculture*, 41(1), 63-75. [https://doi.org/10.1016/S0168-1699\(03\)00042-5](https://doi.org/10.1016/S0168-1699(03)00042-5)

Ojansuu, R., Mäkinen, H. & Heinonen, J. (2018). Including Variation in Branch and Tree Properties Improves Timber Grade Estimates in Scots Pine Stands. *Canadian Journal of Forest Research*, 48(999), 1-12. <https://doi.org/10.1139/cjfr-2017-0435>

Olofsson, K., Holmgren, J. & Olsson, H. (2014). Tree Stem and Height Measurements Using Terrestrial Laser Scanning and the Ransac Algorithm. *Remote Sensing*, 6(5), 4323-4344. <https://doi.org/10.3390/rs6054323>

Osborne, N. L. & Maguire, D. A. (2016). Modeling Knot Geometry from Branch Angles in Douglas-Fir (*Pseudotsuga Menziesii*). *Canadian Journal of Forest Research*, 46(2), 215-224. <https://doi.org/10.1139/cjfr-2015-0145>

Pamerleau-Couture, É., Rossi, S., Pothier, D. & Krause, C. (2019). Wood Properties of Black Spruce (*Picea Mariana* (Mill.) Bsp) in Relation to Ring Width and Tree Height in Even-and Uneven-Aged Boreal Stands. *Annals of Forest Science*, 76(2), 43. <https://doi.org/10.1007/s13595-019-0828-9>

Pan, Y., Birdsey, R. A., Fang, J., Houghton, R., Kauppi, P. E., Kurz, W. A., Phillips, O. L., Shvidenko, A., Lewis, S. L. & Canadell, J. G. (2011). A Large and Persistent Carbon Sink in the World's Forests. *Science*, 333(6045), 988-993. <https://doi.org/10.1126/science.1201609>

Peltola, A. (2014). *Metsätilastollinen Vuosikirja 2014 - Finnish Statistical Yearbook of Forestry 2014*, Finnish Forest Research Institute. 978-951-40-2505-1.

Penman, J., Gytarsky, M., Hiraishi, T., Krug, T., Kruger, D., Pipatti, R., Buendia, L., Miwa, K., Ngara, T., Tanabe, K. & Wagner, F. (2003). Good Practice Guidance for Land Use, Land-Use Change and Forestry. IPCC National Greenhouse Gas Inventories Programme.

Petit, G., Von Arx, G., Kiorapostolou, N., Lechthaler, S., Prendin, A. L., Anfodillo, T., Caldeira, M. C., Cochard, H., Copini, P., Crivellaro, A., Delzon, S., Gebauer, R., Gricar, J., Gronholm, L., Holtta, T., Jyske, T., Lavric, M., Lintunen, A., Lobo-Do-Vale, R., Peltoniemi, M., Peters, R. L., Robert, E. M. R., Roig Juan, S., Senfeldt, M., Steppe, K., Urban, J., Van Camp, J. & Sterck, F. (2018). Tree Differences in Primary and Secondary Growth Drive Convergent Scaling in Leaf Area to Sapwood Area across Europe. *New Phytologist*, 218(4), 1383-1392. <https://doi.org/10.1111/nph.15118>

Pfeifer, N., Gorte, B. & Winterhalder, D. (2004). Automatic Reconstruction of Single Trees from Terrestrial Laser Scanner Data. *Proceedings of 20th ISPRS Congress*, 2004. 114-119.

Piispanen, R., Heinonen, J., Valkonen, S., Mäkinen, H., Lundqvist, S.-O. & Saranpää, P. (2014). Wood Density of Norway Spruce in Uneven-Aged Stands. *Canadian journal of forest research*, 44(2), 136-144. <https://doi.org/10.1139/cjfr-2013-0201>

Pokharel, B., Dech, J. P., Groot, A. & Pitt, D. (2014). Ecosite-Based Predictive Modeling of Black Spruce (*Picea Mariana*) Wood Quality Attributes in Boreal Ontario. *Canadian journal of forest research*, 44(5), 465-475. <https://doi.org/10.1139/cjfr-2013-0252>

Pokharel, B., Groot, A., Pitt, D., Woods, M. & Dech, J. (2016). Predictive Modeling of Black Spruce (*Picea Mariana* (Mill.) Bsp) Wood Density Using Stand Structure Variables Derived from Airborne Lidar Data in Boreal Forests of Ontario. *Forests*, 7(12), 311. <https://doi.org/10.3390/f7120311>

Pothier, D., Fortin, M., Auty, D., Delisle-Boulianne, S., Gagné, L.-V. & Achim, A. (2013). Improving Tree Selection for Partial Cutting through Joint Probability Modelling of Tree

Vigor and Quality. *Canadian journal of forest research*, 43(3), 288-298. <https://doi.org/10.1139/cjfr-2012-0402>

Pretzsch, H. & Rais, A. (2016). Wood Quality in Complex Forests Versus Even-Aged Monocultures: Review and Perspectives. *Wood science and technology*, 50(4), 845-880. <https://doi.org/10.1007/s00226-016-0827-z>

Puliti, S., Saarela, S., Gobakken, T., Ståhl, G. & Næsset, E. (2018). Combining Uav and Sentinel-2 Auxiliary Data for Forest Growing Stock Volume Estimation through Hierarchical Model-Based Inference. *Remote Sensing of Environment*, 204, 485-497. <https://doi.org/10.1016/j.rse.2017.10.007>

Pullen, N., Zhang, N., Dobon Alonso, A. & Penfield, S. (2019). Growth Rate Regulation Is Associated with Developmental Modification of Source Efficiency. *Nature Plants*, 5(2), 148-152. <https://doi.org/10.1038/s41477-018-0357-9>

Racine, E. B., Coops, N. C., St-Onge, B. & Bégin, J. (2013). Estimating Forest Stand Age from Lidar-Derived Predictors and Nearest Neighbor Imputation. *Forest Science*, 60(1), 128-136. <https://doi.org/10.5849/forsci.12-088>

Rathgeber, C. B., Cuny, H. E. & Fonti, P. (2016). Biological Basis of Tree-Ring Formation: A Crash Course. *Frontiers in plant science*, 7, 734. <https://doi.org/10.3389/fpls.2016.00734>

Raumonen, P., Kaasalainen, M., Akerblom, M., Kaasalainen, S., Kaartinen, H., Vastaranta, M., Holopainen, M., Disney, M. & Lewis, P. (2013). Fast Automatic Precision Tree Models from Terrestrial Laser Scanner Data. *Remote Sensing*, 5(2), 491-520. <https://doi.org/10.3390/rs5020491>

Rejou-Mechain, M., Barbier, N., Couteron, P., Ploton, P., Vincent, G., Herold, M., Mermoz, S., Saatchi, S., Chave, J., De Boissieu, F., Feret, J. B., Takoudjou, S. M. & Pelissier, R. (2019). Upscaling Forest Biomass from Field to Satellite Measurements: Sources of Errors and Ways to Reduce Them. *Surveys in Geophysics*, 40(4), 881-911. <https://doi.org/10.1007/s10712-019-09532-0>

Repola, J. (2009). Biomass Equations for Scots Pine and Norway Spruce in Finland. *Silva Fennica*, 43(4), 625-647. <https://doi.org/10.14214/sf.184>

Rune, G. & Warensjö, M. (2002). Basal Sweep and Compression Wood in Young Scots Pine Trees. *Scandinavian Journal of Forest Research*, 17(6), 529-537. <https://doi.org/10.1080/02827580260417189>

Saarela, S., Grafström, A., Ståhl, G., Kangas, A., Holopainen, M., Tuominen, S., Nordkvist, K. & Hyypä, J. (2015). Model-Assisted Estimation of Growing Stock Volume Using Different Combinations of Lidar and Landsat Data as Auxiliary Information. *Remote Sensing of Environment*, 158, 431-440. <https://doi.org/10.1016/j.rse.2014.11.020>

Saarinen, N., Kankare, V., Pyörälä, J., Yrttimaa, T., Liang, X., Wulder, M. A., Holopainen, M., Hyypä, J. & Vastaranta, M. (2019). Assessing the Effects of Sample Size on

Parametrizing a Taper Curve Equation and the Resultant Stem-Volume Estimates. *Forests*, 10(10), 848. <https://doi.org/10.3390/f10100848>

Saarinen, N., Kankare, V., Vastaranta, M., Luoma, V., Pyörala, J., Tanhuanpää, T., Liang, X. L., Kaartinen, H., Kukko, A., Jaakkola, A., Yu, X. W., Holopainen, M. & Hyypä, J. (2017). Feasibility of Terrestrial Laser Scanning for Collecting Stem Volume Information from Single Trees. *ISPRS Journal of Photogrammetry and Remote Sensing*, 123, 140-158. <https://doi.org/10.1016/j.isprsjprs.2016.11.012>

Sanz, B., Malinen, J., Leppänen, V., Valbuena, R., Kauranne, T. & Tokola, T. (2018). Valuation of Growing Stock Using Multisource GIS Data, a Stem Quality Database, and Bucking Simulation. *Canadian Journal of Forest Research*, 48(8), 888-897. <https://doi.org/10.1139/cjfr-2017-0172>

Sasaki, N. & Putz, F. E. (2009). Critical Need for New Definitions of “Forest” and “Forest Degradation” in Global Climate Change Agreements. *Conservation Letters*, 2(5), 226-232. <https://doi.org/10.1111/j.1755-263X.2009.00067.x>

Saukkola, A., Melkas, T., Riekkö, K., Sirparanta, S., Peuhkurinen, J., Holopainen, M., Hyypä, J. & Vastaranta, M. (2019). Predicting Forest Inventory Attributes Using Airborne Laser Scanning, Aerial Imagery, and Harvester Data. *Remote Sensing*, 11(7), 797. <https://doi.org/10.3390/rs11070797>

Schrader, J., Baba, K., May, S. T., Palme, K., Bennett, M., Bhalerao, R. P. & Sandberg, G. (2003). Polar Auxin Transport in the Wood-Forming Tissues of Hybrid Aspen Is under Simultaneous Control of Developmental and Environmental Signals. *Proceedings of the National Academy of Sciences of the United States of America*, 100(17), 10096-10101. <https://doi.org/10.1073/pnas.1633693100>

Sorce, C., Giovannelli, A., Sebastiani, L. & Anfodillo, T. (2013). Hormonal Signals Involved in the Regulation of Cambial Activity, Xylogenesis and Vessel Patterning in Trees. *Plant cell reports*, 32(6), 885-898. <https://doi.org/10.1007/s00299-013-1431-4>

Spicer, R. & Groover, A. (2010). Evolution of Development of Vascular Cambia and Secondary Growth. *New Phytologist*, 186(3), 577-592. <https://doi.org/10.1111/j.1469-8137.2010.03236.x>

Ståhle, S. M., Bruchert, F., Kretschmer, U., Spiecker, H. & Sauter, U. H. (2014). Clear Wood Content in Standing Trees Predicted from Branch Scar Measurements with Terrestrial Lidar and Verified with X-Ray Computed Tomography. *Canadian Journal of Forest Research*, 44(2), 145-153. <https://doi.org/10.1139/cjfr-2013-0170>

Stephenson, N. L., Das, A. J., Condit, R., Russo, S. E., Baker, P. J., Beckman, N. G., Coomes, D. A., Lines, E. R., Morris, W. K., Ruger, N., Alvarez, E., Blundo, C., Bunyavejchewin, S., Chuyong, G., Davies, S. J., Duque, A., Ewango, C. N., Flores, O., Franklin, J. F., Grau, H. R., Hao, Z., Harmon, M. E., Hubbell, S. P., Kenfack, D., Lin, Y., Makana, J. R., Malizia, A., Malizia, L. R., Pabst, R. J., Pongpattananurak, N., Su, S. H., Sun, I. F., Tan, S., Thomas, D., Van Mantgem, P. J., Wang, X., Wiser, S. K. & Zavala, M.

A. (2014). Rate of Tree Carbon Accumulation Increases Continuously with Tree Size. *Nature*, 507(7490), 90-3. <https://doi.org/10.1038/nature12914>

Stovall, A. E., Vorster, A. G., Anderson, R. S., Evangelista, P. H. & Shugart, H. H. (2017). Non-Destructive Aboveground Biomass Estimation of Coniferous Trees Using Terrestrial Lidar. *Remote Sensing of Environment*, 200(1), 31-42. <https://doi.org/10.1016/j.rse.2017.08.013>

Su, Y., Hu, T., Wang, Y., Li, Y., Dai, J., Liu, H., Jin, S., Ma, Q., Wu, J., Liu, L., Fang, J. & Guo, Q. (2020). Large-Scale Geographical Variations and Climatic Controls on Crown Architecture Traits. *Journal of Geophysical Research: Biogeosciences*, 125(2), e2019JG005306. <https://doi.org/10.1029/2019jg005306>

Swatantran, A., Tang, H., Barrett, T., Decola, P. & Dubayah, R. (2016). Rapid, High-Resolution Forest Structure and Terrain Mapping over Large Areas Using Single Photon Lidar. *Scientific reports*, 6, 28277. <https://doi.org/10.1038/srep28277>

Thies, M., Pfeifer, N., Winterhalder, D. & Gorte, B. G. (2004). Three-Dimensional Reconstruction of Stems for Assessment of Taper, Sweep and Lean Based on Laser Scanning of Standing Trees. *Scandinavian Journal of Forest Research*, 19(6), 571-581. <https://doi.org/10.1080/02827580410019562>

Todoroki, C. (1990). Autosaw System for Sawing Simulation. *New Zealand Journal of Forestry Science*, 20(3), 332-348.

Uggla, C., Magel, E., Moritz, T. & Sundberg, B. (2001). Function and Dynamics of Auxin and Carbohydrates During Earlywood/Latewood Transition in Scots Pine. *Plant physiology*, 125(4), 2029-2039. <https://doi.org/10.1104/pp.125.4.2029>

Uggla, C., Moritz, T., Sandberg, G. & Sundberg, B. (1996). Auxin as a Positional Signal in Pattern Formation in Plants. *Proceedings of the National Academy of Sciences of the United States of America*, 93(17), 9282-9286. <https://doi.org/10.1073/pnas.93.17.9282>

Uusitalo, J. (1997). Pre-Harvest Measurement of Pine Stands for Sawing Production Planning. *Acta Forestalia Fennica*, 259(1), 1-56.

Vaganov, E. A., Hughes, M. K. & Shashkin, A. V. (2006). *Growth Dynamics of Conifer Tree Rings: Images of Past and Future Environments*, Springer Science & Business Media. 3540312986.

Vauhkonen, J. & Packalen, T. (2018). Uncertainties Related to Climate Change and Forest Management with Implications on Climate Regulation in Finland. *Ecosystem Services*, 33, 213-224. <https://doi.org/10.1016/j.ecoser.2018.02.011>

Vauhkonen, J., Tokola, T., Packalén, P. & Maltamo, M. (2009). Identification of Scandinavian Commercial Species of Individual Trees from Airborne Laser Scanning Data Using Alpha Shape Metrics. *Forest Science*, 55(1), 37-47.

Vuoristo, I. (1937). Havupuumetsien Laatuvarvo ja Laadun Arviointi. *Silva Fennica*, 39, 232-247.

Wang, Y. S., Hyypä, J., Liang, X. L., Kaartinen, H., Yu, X. W., Lindberg, E., Holmgren, J., Qin, Y. C., Mallet, C., Ferraz, A., Torabzadeh, H., Morsdorf, F., Zhu, L. L., Liu, J. B. & Alho, P. (2016). International Benchmarking of the Individual Tree Detection Methods for Modeling 3-D Canopy Structure for Silviculture and Forest Ecology Using Airborne Laser Scanning. *IEEE Transactions on Geoscience and Remote Sensing*, 54(9), 5011-5027. <https://doi.org/10.1109/Tgrs.2016.2543225>

Warensjö, M. & Rune, W. (2004). Stem Straightness and Compression Wood in a 22-Year-Old Stand of Container-Grown Scots Pine Trees. *Silva Fennica*, 38(2), 143-153. <https://doi.org/10.14214/Sf.424>

Wästlund, A., Holmgren, J., Lindberg, E. & Olsson, H. (2018). Forest Variable Estimation Using a High Altitude Single Photon Lidar System. *Remote Sensing*, 10(9), 1422. <https://doi.org/10.3390/rs10091442>

Wei, Q., Leblon, B. & La Rocque, A. (2011). On the Use of X-Ray Computed Tomography for Determining Wood Properties: A Review. *Canadian journal of forest research*, 41(11), 2120-2140. <https://doi.org/10.1139/X11-111>

West, G. B., Brown, J. H. & Enquist, B. J. (1999). A General Model for the Structure and Allometry of Plant Vascular Systems. *Nature*, 400, 664-667. <https://doi.org/10.1038/23251>

White, J. C., Wulder, M. A., Varhola, A., Vastaranta, M., Coops, N. C., Cook, B. D., Pitt, D. & Woods, M. (2013). A Best Practices Guide for Generating Forest Inventory Attributes from Airborne Laser Scanning Data Using an Area-Based Approach. *Forestry Chronicle*, 89(6), 722-723. <https://doi.org/10.5558/tfc2013-132>

Wilkes, P., Lau, A., Disney, M., Calders, K., Burt, A., De Tanago, J. G., Bartholomeus, H., Brede, B. & Herold, M. (2017). Data Acquisition Considerations for Terrestrial Laser Scanning of Forest Plots. *Remote Sensing of Environment*, 196(1), 140-153. <https://doi.org/10.1016/j.rse.2017.04.030>

Wylie, R. R., Woods, M. E. & Dech, J. P. (2019). Estimating Stand Age from Airborne Laser Scanning Data to Improve Models of Black Spruce Wood Density in the Boreal Forest of Ontario. *Remote Sensing*, 11(17), 2022. <https://doi.org/10.3390/rs11172022>

Yrttimaa, T., Saarinen, N., Kankare, V., Liang, X., Hyypä, J., Holopainen, M. & Vastaranta, M. (2019). Investigating the Feasibility of Multi-Scan Terrestrial Laser Scanning to Characterize Tree Communities in Southern Boreal Forests. *Remote Sensing*, 11(12), 1423. <https://doi.org/10.3390/rs11121423>

Yu, X. W., Hyypä, J., Karjalainen, M., Nurminen, K., Karila, K., Vastaranta, M., Kankare, V., Kaartinen, H., Holopainen, M., Honkavaara, E., Kukko, A., Jaakkola, A., Liang, X. L., Wang, Y. S., Hyypä, H. & Katoh, M. (2015). Comparison of Laser and Stereo Optical, Sar and Insar Point Clouds from Air- and Space-Borne Sources in the Retrieval of Forest

Inventory Attributes. Remote Sensing, 7(12), 15933-15954.
<https://doi.org/10.3390/rs71215809>

Zeller, L., Ammer, C., Annighöfer, P., Biber, P., Marshall, J., Schütze, G., Del Río Gaztelurrutia, M. & Pretzsch, H. (2017). Tree Ring Wood Density of Scots Pine and European Beech Lower in Mixed-Species Stands Compared with Monocultures. *Forest Ecology and Management*, 400, 363-374. <https://doi.org/10.1016/j.foreco.2017.06.018>

Zhang, S. (1995). Effect of Growth Rate on Wood Specific Gravity and Selected Mechanical Properties in Individual Species from Distinct Wood Categories. *Wood Science and Technology*, 29(6), 451-465. <https://doi.org/10.1007/Bf00194204>

Zobel, B. (1984). The Changing Quality of the World Wood Supply. *Wood Science and Technology*, 18(1), 1-17. <https://doi.org/10.1007/Bf00632127>

Zobel, B. J. & Jett, J. B. (2012). *Genetics of Wood Production*, Springer Science & Business Media. 3642795145.

(191 references)